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THE SYSTEMATICS OF THE AMERICAN SPECIES OF *ALNUS* (BETULACEAE)¹

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INTRODUCTION

All of the American species of *Alnus* are morphologically variable, and in several cases they are polymorphic. Many species and infra-specific taxa, in addition, are neither morphologically nor genetically well-differentiated. Taxa which are isolated geographically or ecologically pose few problems, but when their ranges intersect or overlap, they often become more difficult. Nevertheless, the taxa are all distinguishable, though the simultaneous use of several different characters may sometimes be required for accurate determinations.

The literature dealing with the genus in North America reveals considerable confusion in the circumscriptions, ranks, and classification of taxa at all infrageneric levels. Single-character variants have repeatedly been treated as distinct species, subspecies, or varieties, and there have been no unified concepts of these taxa. In order to confront these problems, I have assembled data from a number of sources not previously used in revisions of *Alnus*, including numerical taxonomic and chemosystematic studies. The detailed results of this experimental work will be discussed separately in a later paper.

The purpose and scope of this work is primarily monographic; the experimental aspects were conducted solely for the data they could provide and not as ends in themselves. In the work as a whole, traditional taxonomic methods predominated; that is, data were

¹Editor's note: this is part one of two. Part II, including the remainder of the Taxonomic Treatment and all references, will be published in Vol. 81, No. 826 (April, 1979).

collected from a wide variety of sources, herbarium and field studies were undertaken in order to gain an intimate familiarity with the group, and, finally, the most phylogenetically accurate as well as practical system possible was synthesized.

The genus *Alnus* is not particularly large, but in order to perform a comprehensive investigation, I limited the present study to those taxa occurring in the New World. Thus I was able to see all of the species in the field and to obtain an ample supply of herbarium and experimental material. In instances where species occur in both the New and Old Worlds, as much material from the Old World as could be obtained was used.

Considerable work remains to be done, especially with regard to the Latin American taxa (for which herbarium material is not abundant). I feel that I have made significant improvements in the classification of these taxa, but the system proposed here must be regarded as somewhat tentative, pending additional exploration of the areas in which they occur and the accumulation of a great deal more material. In all of the species and infraspecific taxa, more detailed study of individual populations will have to be made before a true understanding of this group can be achieved. Especially important will be genetic and cytogenetic investigations, which are practically nonexistent. The present work should provide a basis, in terms of both classification and nomenclature, for such future investigation.

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HISTORICAL ACCOUNT

Although *Alnus* was regarded as a distinct genus by Tournefort (1700) and most others before him, Linnaeus included it as a single species of *Betula* in the first edition of *Species Plantarum* (1753). This treatment was not widely accepted, however, and the separate genera continued to be used by such authors as Miller, Hill, and Ehrhart. Miller, in the 7th edition of *The Gardener's Dictionary* (1759) wrote: "Dr. *Linnaeus* has joined this Genus to the *Betula*, and places it in the fourth Division of his twenty-first Class of Plants, intitled, *Monaecia tetrandria*, from the Plants having male and female flowers, and the male having four Stamina. But as the Fruit

of the Alder is of a conical Form, and that of the Birch cylindrical, so we shall keep them separate, whereby the Work will be rendered more intelligible to the Generality of Readers." The compound name *Betula-Alnus* was used for the alders in 1770 by Weston and in 1785 by Marshall (the genus *Betula* being retained in both cases for the birches). Above the level of genus, *Alnus* was included with such gymnospermous cone-bearing trees as *Abies*, *Pinus*, and *Larix* by Ray (1682) and Tournefort (1700). The development of supra-generic concepts applying to the alders is reviewed by Stearn (1973).

The genus was first divided into segregate genera in the revision by Spach (1841) who separated *Alnaster* and *Clethropsis* from *Alnus*, those segments being equivalent to the subgenera recognized in the present treatment. *Alnaster* included only *A. viridis*; *Clethropsis*, *C. nitida* and *C. nepalensis*, two Asiatic species; and *Alnus* the remaining species. Spach separated the South American species of *Alnus* into sect. *Phyllothyrsus* and the remaining species into sect. *Gymnothyrsus*, disregarding the great similarity between *A. acuminata* and the Mexican and Central American taxa.

The next revision of the genus was the monograph of Regel (1861), who viewed the genus as a single unit, but divided it into sections corresponding to Spach's genera and sections. In this work *Alnus jorullensis* was first treated as a variety of *A. acuminata*. *Alnus serrulata* was treated as a variety of the European *A. glutinosa*, and *A. rubra* was considered a variety of *A. incana*. Elements of *A. incana* ssp. *rugosa* were included in both *A. incana* and *A. glutinosa*. In 1865 Regel completed a second revision of the genus in which he used subgenera instead of sections as his major infrageneric divisions and changed many names and circumscriptions as well. Here he recognized *A. jorullensis*, *A. rubra*, and *A. serrulata* as separate species; the treatment of *A. incana* ssp. *rugosa* remained confused as before. *Alnus maritima* appeared in the second of Regel's works, but was placed in his subg. *Gymnothyrsus* rather than in subg. *Clethropsis*. A third treatment by Regel appeared in de Candolle's *Prodromus* (1868) and closely followed his 1865 system except for a return to the use of sections rather than subgenera.

Winkler revised the genus in *Das Pflanzenreich* in 1904. In this treatment only two sections are recognized, sect. *Alnobetula* (equivalent to Spach's genus *Alnaster*) and sect. *Gymnothyrsus* (including Spach's genus *Clethropsis*). Major changes introduced in this work

include the use of the names *Alnus alnobetula* (for *A. viridis*), *A. rugosa*, and *A. tenuifolia*. *Alnus serrulata* was treated as a variety of *A. rugosa*, and all of the Latin American taxa were considered varieties of *A. jorullensis*.

Although not monographic, several important revisionary works by Callier appeared about this time (1892, 1904, 1911, & 1918). In these publications a large number of new names and combinations are found.

The most recent revisions of the genus are those of Czerepanov (1955) and Murai (1964). Czerepanov erected an intricate structure of genera, sections, subsections, series, and species, but he did not make many real changes in the previous systems. Several of his groupings are quite artificial, such as the placing of *Alnus serrulata* in the same section as *A. rhombifolia* while putting *A. incana* ssp. *rugosa* in another section, and show a lack of understanding of the taxa, as in the recognition of both *A. tenuifolia* and *A. densiflora* as species. In a few cases, however, his choices seem to be wise, including the close placement of *A. jorullensis* and *A. firmifolia* in the same series. Murai's treatment (1964) is the most recent for the genus, but unfortunately it is practically unobtainable in American libraries. In an earlier version, Murai (1963) recognized two genera, *Alnaster* and *Alnus*, but in 1964 he combined these into one genus with two subgenera and six sections. That treatment follows popular current usage fairly closely, but it differs in several important respects. First, Murai treats *Alnus crispa* and *A. sinuata* as subspecies of a single species, *A. crispa* (the treatment used by Hultén, 1944). Second, he attempts to show a very close phylogenetic relationship between the Latin American and eastern Asian species by placing them all in sect. *Japonicae* of subg. *Gymnothyrsus* (probably not a correct interpretation). Third, he recognizes the close relationship of *Alnus maritima* with the Asian species of his sect. *Clethropsis*.

The most neglected aspect of the taxonomy of *Alnus* in the New World involves the complex of species and infraspecific taxa of Latin America. Besides the original descriptions of these taxa and more or less superficial treatments in the monographs and revisions listed above, the only study of this group has been the work of Fernald (1904b), Bartlett (1909), and Standley (1920), all based solely on a very limited supply of herbarium material.

TAXONOMIC CONCEPTS

The alders form a well-defined group easily circumscribed on the basis of morphological similarities and discontinuities. Although they have sometimes been segregated into a number of separate genera, as discussed above, the species share many features distinctive to the group as a whole and should properly be treated as a single genus. This view is widely accepted today. *Alnus* is separated from its closest ally, *Betula*, by several major discontinuities, including its woody infructescences with persistent scales, the structure of its buds, and the number of stamens in the flowers. Within the genus there are three distinct evolutionary lines, these being treated here as subgenera and distinguishable on the basis of leaf venation, exposure of the pistillate catkins during the winter, structure of the buds, season of blooming, and flower structure. One can find still smaller natural groups of species within the subgenera, but these are not as distinct morphologically, and it does not seem useful to subdivide the subgenera into sections.

Species in *Alnus* consist of apparently allogamous populations, these often showing incomplete intrinsic reproductive barriers among themselves (at least within subgenera), but usually isolated by their habitats. In spite of a relatively high level of morphological variability, especially in vegetative features, the species are nevertheless rather easily distinguished on the basis of morphology.

Previous workers have described numerous species and infraspecific taxa on the basis of variation in the shape, margin, pubescence, and gland characteristics of the leaves of already-known species in the genus. When a large number of specimens from throughout the ranges of such taxa are examined, however, these features are nearly always found to vary continuously from one extreme to the other without clear breaks. Taxa that were based mainly on extremes in pubescence (*Alnus crispa* var. *mollis*, *A. ferruginea*, *A. pringlei*, *A. rhombifolia* var. *bernardina*, *A. rugosa* f. *emersoniana*, *A. serrulata* f. *noveboracensis*), leaf shape (*A. arguta* var. *subsericea*, *A. crispa* var. *harricanensis*, *A. ovalifolia*, *A. serrulata* var. *subelliptica*), and infructescence form (*A. crispa* var. *elongata*) are consequently no longer recognized.

It has been suggested by Raven (1962) that the degree of

reproductive isolation between taxa where they come into contact is of fundamental taxonomic importance, providing information dealing with the relationship between groups of plants as they actually occur in nature. Groups which intergrade in such areas are considered to be subspecies of the same species, while populations which may hybridize but do not intergrade are treated as separate species (*loc. cit.*). This concept is a useful one in *Alnus*, and it has been applied in the present treatment.

In several instances wide-ranging species have been treated previously as separate species where they occur in different geographical regions. From the degree of morphological similarity between the populations in these regions and the amount of intergradation seen where their ranges overlap, it is evident that these taxa are conspecific. *Alnus tenuifolia* in western North America, *A. rugosa* in eastern North America, and *A. incana* in Eurasia are seen as representing parts of a single species, as are *A. crispa* in eastern and northern North America, *A. sinuata* in western North America, and *A. viridis* in Eurasia. In Latin America, the same pattern is shown by *A. arguta* in Mexico and Central America and *A. acuminata* in South America. In these taxa, however, in spite of the clear relationships at the species level, one can see a degree of differentiation in each case. The geographically separated populations are therefore considered to be subspecies of *A. incana*, *A. viridis*, and *A. acuminata*, respectively.

Subspecies, as employed in the present treatment, are segments of species having relatively large geographical ranges and which are distinct in morphology and (to at least some degree) habitat (cf. Du Rietz, 1930; Camp & Gilly, 1943; Mayr, 1947; Steenis, 1957). The category is used not only for those taxa showing distinct geographical distributions, but also for ecotypes, as seen in *Alnus acuminata* spp. *arguta* and *glabrata* and *A. jorullensis* spp. *jorullensis* and *lutea*. The biological nature of geographical and ecological races in *Alnus* appears to be essentially the same, warranting the use of the same formal category.

Putative hybridization frequently occurs where closely related species of *Alnus* grow sympatrically (e.g., *A. incana* ssp. *rugosa* and *A. serrulata*). In such cases, the taxa are otherwise morphologically distinct and do not appear to intergrade except for the occurrence of intermediate individuals in the putative hybrid populations. Many

species of *Alnus* are extrinsically isolated, as shown by successful artificial hybridization between such distinct and isolated taxa as *A. glutinosa* of western Europe and *A. rubra* of western North America (Ljunger, 1959).

EVOLUTION AND PHYTOGEOGRAPHY

Alnus is distributed throughout the Northern Hemisphere, extending below the Equator along the Andes in South America. It is absent from the Antilles in both modern and fossil floras, though floristically related genera (*Fagus*, *Salix*, *Myrica*, *Liquidambar*, and *Nyssa*) existed there in the Tertiary (Graham, 1972b). Distributional centers can be recognized in the following regions: 1) circumpolar Europe, Asia, and North America, 2) mountainous southern Europe, Asia Minor, and Iran, 3) the Himalayas and adjacent mountainous central China, 4) coastal eastern Asia from northern Manchuria to the Tropic of Cancer, 5) mountainous parts of Mexico, Central America, and northern South America, 6) coastal eastern North America from Nova Scotia to the Gulf of Mexico, and 7) western North America from southern Alaska to northern Mexico. In addition, alleged fossils of *Alnus* have been reported from Australia and Tasmania, where the genus does not occur today, but these are of questionable identity (Berry, 1923).

Alnus is represented in the early fossil record of the angiosperms, appearing in the upper Cretaceous, where it was associated with other early woody genera, including *Betula*, *Acer*, *Corylus*, *Cercis*, *Ginkgo*, and *Sequoia*. The earliest "definite *Alnus* pollen" in North America appears in the Maestrichtian of the Rocky Mountains, and the first mega-fossils are of the same age in British Columbia (Wolfe, 1973). During the Tertiary the genus became prominent and is represented by wood, leaves, fruits, cones, and pollen in numerous fossil floras. Over 40 Cenozoic species are recognized by LaMotte (1952) for North America alone. Pollen of *Alnus* is common in bog deposits of Pleistocene age and is an indicator of changes in climate and vegetation during that period. Many Cenozoic fossil alders bear a striking resemblance to present-day species, and it may be possible to trace the migrations and evolution of these taxa using such evidence, although the record is somewhat sketchy.

Origin of the Genus and Subgenera.

According to Takhtajan (1969), *Alnus* may have evolved in southwestern Asia. He shows that subg. *Clethropsis* (which he considers to be the most primitive segment of the genus) is presently more or less restricted to the Himalayas, Assam, and southwestern China, a region he believes to have been important in early angiosperm evolution. However, recent evidence, summarized by Raven and Axelrod (1972, 1974), points away from this region as the site of early angiosperm evolution. These authors (1974) conclude that the angiosperms most likely originated in western Gondwanaland before the separation of Africa and South America, spreading northward from this region into Laurasia, where the Hamamelidiflorae (including the Fagales) then differentiated. Furthermore, as discussed below, much evidence suggests that subg. *Clethropsis* may not actually be the most primitive aspect of the genus after all.

Murai (1964) states that *Alnus* originated in eastern Asia, specifically in an area including or near present-day Japan, basing this conclusion on the large total number of species and the large number of supposedly relict distributions occurring there today. He regards members of his sect. *Bifurcatus* (of subg. *Alnobetula*), today completely restricted to Japan, as the most primitive taxa of the genus. There is evidence, however, that while this area, like the Himalayan region, has been an important center of preservation, it was not a major center of angiosperm evolution (Raven & Axelrod, 1974).

It is difficult to deduce the true site of origin of *Alnus* on the basis of present information. A number of methods have been proposed for locating possible points of origin or centers of dispersal of plant groups, including the use of measures of diversity, degree of differentiation, size of area, presence of disjunct distributions, and fossil evidence. Various reviews of these techniques (e.g., Cain, 1944; Cracraft, 1975) have shown that none is completely satisfactory for all taxa. But one or more of them may be useful in a particular group. All of the above criteria, and especially the principle that the greatest diversity in a group of plants occurs in the area of its origin (Vavilov, 1951), suggest that the genus did, in fact, originate on the Asian land mass. Present distributional patterns

and the fossil record indicate that subg. *Clethropsis* evolved in southern Asia, while subg. *Alnobetula* differentiated in northern and northeastern Asia. Subgenus *Alnus*, considered here to be the most primitive part of the genus, most likely originated at southern and mid-latitudes in Asia, later further specializing in cooler, more northern areas. Following this original divergence, each of the subgenera spread throughout the Northern Hemisphere.

On the basis of wood anatomy, it appears that the Betulaceae arose from an ancient Hamamelidaceous stock derived from Magnoliaceous ancestors (Tippo, 1938). Wolfe (1973), in discussing the origin of patterns of leaf venation in the Amentiferae, supports this view, stating: "in their consistent craspedrodromy and intercostal venation, the various members of the Betulaceae are highly similar to the *Corylopsis* type and could well be the end products of this hamamelid line". Continuing, he shows that the leaf venation of the Betulaceae (*Corylus* pattern) is entirely absent from the Magnoliidae, Dilleniidae, and Asteridae, and is rare in the Rosidae. In the Hamamelidae, however, it is common in the Fagaceae and Ulmaceae as well as the Betulaceae. Early in the history of the family, *Betula* and *Alnus* apparently formed one line while *Corylus*, *Ostrya*, *Ostryopsis*, and *Carpinus* diverged and formed another. *Betula* and *Alnus*, on the basis of anatomical features, have been shown to be the most primitive members of the family (Tippo, 1938; Hall, 1952). As seen from their similar morphology and anatomy, these two genera show relatively little divergence.

An early hypothesis as to the events which may have followed the evolution of *Alnus* is outlined by Kryshstofovich (1929). According to this theory, the early Tertiary flora of Europe became divided into three principal "floristic provinces". The northwestern division forest (Greenland Province) was made up of *Populus* species and other temperate deciduous trees showing no Asiatic relationship. *Alnus* and *Betula* were rare in this region during the early Tertiary. The second region (Turgai Province) occupied the middle zone of Siberia, America, and Alaska, and it was covered by deciduous forest in which *Betula* and *Alnus* occupied an important place. To the south was the third region (Poltava Province) which included the Ukraine and southern Russia, and which was characterized by remnants of the older evergreen tropical vegetation. As the climate cooled, the Turgaian vegetation enlarged, spreading into the Greenlandian and Poltavan regions. Thus, the fossil record was inter-

preted by Kryshstofovich as showing that *Alnus* originated in the southern Asian highlands, spreading east across Siberia and western North America, but not moving west until later in the Tertiary to complete the circumpolar distribution seen today. In fact, the present distribution and fossil record of *Alnus* in North America do suggest such an early introduction from the west followed by a much more recent migration from the east.

The species comprising subg. *Alnus* are divided into two sections by Murai (1964), one of these (sect. *Japonicae*) including several eastern Asian taxa as well as all of the Latin American taxa, and the other (sect. *Glutinosae*) including *A. incana* and its various allies. Murai concludes that both of the sections originated in the vicinity of Japan, sect. *Japonicae* directly from his sect. *Clethropsis*, and sect. *Glutinosae* from ancestors common to itself and sect. *Clethropsis*. All of the evidence, however, suggests that subgenera *Alnus* (sects. *Glutinosae* and *Japonicae* of Murai) and *Clethropsis* are monophyletic, which would make the derivation of Murai's sections in this manner impossible. Murai's sect. *Glutinosae* appears, rather, to be derived from his sect. *Japonicae* and adapted to a cooler climate. Close relationships between taxa of eastern Asia and northern Latin America were first noted by Hara (1948) and later discussed briefly by Matuda (1953) and Sharp (1953a, 1972). Pollen said to resemble that of *Alnus japonica* has been reported from the early Oligocene of Colorado by Van Alstine (1969), though it seems doubtful that such an identification could be made with much precision. Comparative morphology does not substantiate the relationship suggested by Murai between the alders of Mexico and eastern Asia. Additional study will be needed to establish the true relationship.

Dispersal in the New World

Axelrod and Raven (1972), in discussing plate tectonic theory and evolutionary biogeography, hypothesize that the Amentiferae had its primary radiation on the Laurasian land mass before Europe and America were separated by the North Atlantic Ocean. They conclude that "migration across Laurasia was direct and essentially uninterrupted during much of the Cretaceous . . ." This connection between Europe and America may have lasted well into the Eocene

(cf. Raven, 1972; Ryan & Axelrod, 1974). However the evidence seems to point away from an early introduction of *Alnus* from the east, as discussed below.

Alnus has generally been regarded as a remnant of widespread mesophytic Arcto-Cretaceous and Arcto-Tertiary geofloras (Axelrod, 1952). However Wolfe (1972) has questioned the validity of the concept of a uniform mesophytic flora in the early Tertiary on the basis of paleobotanical data, noting that "no known Cretaceous or Paleocene flora contains 20 or more mixed mesophytic genera." Pollen data suggest the existence of two major floristic provinces during the late Cretaceous and early Tertiary, the first including eastern North America and Europe, and the second occupying western North America and eastern Asia (Wolfe, 1975). *Alnus* may first have been represented in the tropical vegetation, and not become a component of the temperate forest until the Oligocene (Wolfe, 1972). During warmer periods in the Oligocene the alders, along with the maples and other such presently temperate genera, are seen as again occupying lowland regions. Cooler climates following this period removed the tropical vegetation, though a true mixed mesophytic vegetation did not appear until the Miocene (Wolfe, 1972).

In discussing the vegetational history of the Rocky Mountains, Leopold and MacGinitie (1972) show affinities between the early Eocene floras of this region and modern plants of southeastern Asia. However, Raven and Axelrod (1974) point out that this Rocky Mountain fossil flora could just as easily represent a remnant of an older widespread subtropical Laurasian vegetation as a flora with such southeastern Asian connections. Chaney (1947) shows that during Eocene time the neotropical flora extended north to about 49 degrees on the western edge of the continent. The flora of the Rocky Mountains had taken on a tropical American aspect by mid-Eocene, while in far northwestern America the termination of Asiatic affinities was more gradual, lasting until mid-Miocene, by which time the modern coniferous forest had already developed in the Rocky Mountains (Leopold & MacGinitie, 1972).

According to Graham (1972a), the lower Tertiary vegetation of the southern United States probably consisted of neotropical warm-temperature to tropical elements with some broad-leaved deciduous species (including *Alnus*), while a broad-leaved deciduous community with paleotropical components existed in the Pacific North-

west. After the Palaeogene, the Rocky Mountain and western floras lost their Asiatic element, which was gradually replaced by an expanding mixed mesophytic forest in mid-Tertiary. Later, mountain building resulted in changing climates, eliminating the mixed mesophytic element in much of the western United States, Canada, and western Europe.

The ancestors of both *Alnus maritima* and the present Latin American species were doubtless components of the early Tertiary vegetation of America, having arrived from Asia via the Bering land bridge, although Murai (1964) shows *A. maritima* entering by a route through southeastern Asia and South America before the division of Gondwanaland, an idea not in accord with the fossil evidence (see below). Although fossils of *Alnus* from Latin America are few, enough exist to show that the genus reached this region from the north at a relatively early time. Using a fossil pollen flora from Veracruz, Graham (1972b, 1973) shows that *Alnus* (along with *Abies*, *Juglans*, *Fagus*, *Liquidambar*, *Ulmus*, *Celtis*, *Picea*, *Myrica*, and *Populus*) reached southern Mexico by the mid-Miocene but is not present in older sediments there. Three genera from this flora (*Alnus*, *Juglans*, and *Myrica*) are found in late Miocene pollen deposits in Panama, being absent from earlier floras there. The earliest abundant *Alnus* pollen in northern South America is mid-Pleistocene in age, although infrequent, isolated grains are also found in lower Pleistocene sediments (Hammen, 1972; Graham, 1972b, 1973). A Pliocene species based on leaf material from Bolivia (*Alnus preacuminata*) was published in 1922 by Berry and is often cited in connection with the southward migration of northern temperate genera, but this fossil is not generally accepted today as representing *Alnus*. Pollen of *Myrica* appears in South America before *Alnus* (in the lower Pliocene), but *Juglans* is not found until the lower Quaternary (Graham, 1972b). By the middle to late Jurassic, orogenies had produced islands between North and South America, but presumably *Alnus* did not migrate south, at least in numbers, until the last fold of the isthmus (Talamanca Ridge) became fully emerged in the Miocene (Bartlett & Barghoorn, 1973).

Alnus viridis and *A. incana* may not have been introduced to North America until after the Miocene, when the northern climate became cooler. *Alnus viridis* ssp. *crispa* and *A. incana* ssp. *rugosa* may be the most primitive segments of these species, both existing as apparent relicts in northeastern North America today. The origin of

A. serrulata is obscure, but it undoubtedly occurred at a very early time. It, like *A. maritima*, may be a remnant of the early Tertiary flora, but its affinity to *A. incana* suggests a later origin, perhaps in the Miocene or Pliocene. *Alnus rubra* appears to be a remnant of the western mesophytic Miocene forest, as are *A. rhombifolia*, *A. oblongifolia*, and the species of the Latin American complex. The stock which formed this group moved south into Mexico and Central America, where it diverged to form the taxa seen in those regions today.

Historical Factors Affecting Distributions.

Of the present alders occurring in eastern North America, other than *Alnus maritima*, *A. serrulata* appears to be the most ancient, judging from its high degree of morphological specialization. The species today has a predominantly coastal distribution, although it occurs in the Appalachian and Ozark highlands as well, where it may have evolved. Braun (1955) points out that there are many disjunctions of vegetation from upland areas (the Appalachian and Interior Highlands) on the younger Atlantic Coastal Plain and explains that these occurred during the Tertiary, followed by dissection of the intermediate peneplane, which resulted in the loss of suitable habitats there. During the Pleistocene glacial periods, the range of *A. serrulata* may have been decreased in the north, especially in the mountains. Braun (1951) feels that glaciation did not strongly disrupt the deciduous forest zone in the southeastern United States as far north as the Appalachian Plateau in southern Ohio and Kentucky. Evidence from numerical analysis (Furlow, in preparation) suggests that *A. serrulata* survived the Pleistocene in two widely-separated localities, the southeastern Atlantic Coastal Plain and the Ozark Highlands, where the populations have diverged significantly.

Alnus viridis ssp. *crispa* must have been separated from *A. viridis* of Europe more recently, as shown by the relatively very small divergence of these taxa. Hultén (1963) argues that the North Atlantic floras are very ancient, and that "the phytogeographical conditions around the North Atlantic . . . give poor support for a land bridge that could have existed in Quaternary or late Tertiary times." He allows, however, that "circumpolar plants of the far North" probably migrated by wind over the frozen polar sea or on

floating ice. It would not be difficult to imagine *Alnus* being dispersed in this manner. This taxon probably survived glacial advances in several refugia, including the southern Appalachians, where it occurs as a relict today. A. Löve (1959, 1967) and Löve and Löve (1967) provide evidence that refugia existed in parts of Scandinavia, Iceland, and the Canadian arctic archipelago west of Baffin Island, and Ives (1963) concludes that large parts of northern Labrador, where ssp. *crispa* occurs today, remained ice-free during the maximum extent of Wisconsin glaciation. That the species could have withstood the severe conditions of the Pleistocene in such northern refugia is shown by Thorarinsson (1963), who cites fossil alder leaves in Pleistocene volcanic sediments in Iceland.

Harshberger, as early as 1903, rejected the idea of massive migrations of plants before advancing Pleistocene glaciers and accepted the Appalachians as a glacial refugium in the eastern United States. The Scandinavian element, according to him, invaded the New World in the late Pleistocene, remaining after the final glacial retreat. *Alnus incana* ssp. *rugosa*, which is scarcely differentiated from *A. incana* of southwestern Europe, could have arrived in this way, but if so, the populations of *A. incana* present in Scandinavia today must have displaced the Pleistocene forms by migrating from the east at a later time since these are quite different from either ssp. *rugosa* or *incana* of southwestern Europe, as shown below. It is possible that ssp. *rugosa* entered the New World at an earlier period, that ssp. *incana* then became extinct in northern Europe, and that the present northern European ssp. *incana* stock invaded Scandinavia from the east, all before the Pleistocene. Subspecies *rugosa* probably survived in refugia at low elevations, either east or west of the Appalachian highlands and immediately south of the ice (D. Löve, 1959).

It has been shown by Hultén (1928) from the distributions of a number of species that a flow of plants has occurred in both directions between Siberia and North America. *Alnus incana* ssp. *tenuifolia* and *A. viridis* ssp. *sinuata* apparently entered this region following the extinction of the mixed mesophytic forest in the middle Miocene, because their first fossils are in the Miocene of Alaska (Wolfe, 1969). Fossil species corresponding to these present taxa, *A. harneyana* and *A. fossilis* (*A. carpinoides*), respectively, were present in the western United States and Canada during the Miocene in habitats similar to the ones they have today (Chaney,

1959; Chaney & Axelrod, 1959). During the Pleistocene *A. incana* ssp. *rugosa* was separated from ssp. *tenuifolia* and *A. viridis* ssp. *crispa* from ssp. *sinuata* by a "wide gap in the continuity of the northern coniferous forest" (Raup, 1947). Subspecies *sinuata* may have survived the glacial advances in refugia in unglaciated Alaska (Hultén, 1937b; Livingstone, 1955) and points southward to Washington (Heusser, 1960) as well as in its present habitats in the mountains of the northwestern United States, though probably at lower elevations. Its Pleistocene presence in these localities is supported by geological, paleobotanical, and botanical evidence (Heusser, 1960). *Alnus incana* ssp. *tenuifolia* probably survived in its present habitats in the Sierra Nevada and Rocky Mountains as far south as New Mexico and Arizona. After the Pleistocene, *A. incana* ssp. *rugosa* again extended across northern Canada and met ssp. *tenuifolia* in northern Alberta or Saskatchewan. At the same time, the range of *A. viridis* ssp. *crispa* became continuous with that of ssp. *sinuata* in Alaska.

Alnus incana spp. *rugosa* and *tenuifolia* fit the pattern shown by Iltis (1966) in which western species range north and south across the glacial boundary while their eastern vicariants are restricted to glaciated land. Iltis interprets this pattern as evidence for the ultimate western origin of these eastern taxa, but in this case at least, it seems more likely that the restriction of ssp. *rugosa* to glaciated soil in the eastern United States and Canada is an artifact caused by climate. In the mountainous West, ssp. *tenuifolia* occurs south of the glacial boundary only at high elevations in the mountains or in the far North. The cool climatic conditions required by *A. incana* do not exist south of the glacial boundary in the East. In fact, a considerable amount of glaciated land exists south of the southern limits of the range of *A. incana* ssp. *rugosa* in eastern North America.

It is probable that *Alnus maritima* was formerly much more widespread in North America than it is today. Its closest allies are found only in Asia, following a pattern shared by many other woody genera of eastern North America and that region (Li, 1971, 1972). Other members of subg. *Clethropsis* are known in the fossil record of the western United States and Canada. These taxa have the same distinctive leaf features (margin and venation) of modern representatives of this group. One such species, *Alnus relatus*, occurred in Idaho and Oregon during the Miocene in habitats similar to those of

A. maritima in the eastern United States today (Chaney, 1959). Another fossil species, *A. cremastogynoides*, described from the Eocene or Oligocene of British Columbia, differs in certain respects, but also shows the characteristic leaf features of this group (cf. Berry, 1926; Brown, 1937).

The presence of *Alnus maritima* on the Delaware Peninsula might best be regarded as of relatively recent achievement since this species is not hardy further north and probably could not have survived the Pleistocene there. It most likely migrated to its present location on the coastal plain during the climatic moderation following the Pleistocene glaciation from some location further to the south. The cause of the wide disjunction of this species in Delaware and Oklahoma is not known, but the two populations are shown in the numerical taxonomic and chemosystematic studies (below) to have diverged somewhat, pointing away from a recent achievement of the disjunction (cf. Fryxell, 1967). This evidence, together with the indications of great antiquity discussed above, indicates an origin of the disjunct distribution by isolation of the populations following range restriction.

The Latin American taxa, along with *Alnus rubra*, *A. rhombifolia*, and *A. oblongifolia*, apparently have been in their present locations for a very long time, as suggested by McVaugh (1952). *Alnus rubra*, today restricted to the Pacific coastal fog belt, appears to be a relict from the moist mixed forest of the Northwest in the Miocene. *Alnus rhombifolia* may have also been a part of this forest, having adapted to summer-dry conditions since the Pleistocene (Wolfe, 1969). Miocene fossils of *Alnus hollandiana* (*A. corrollina*), a species morphologically similar to modern *A. rhombifolia*, are described from western lowland and slope forests by Chaney (1959), in association with such mesophytic genera as *Acer*, *Fraxinus*, *Fagus*, *Ulmus*, *Liquidambar*, *Ostrya*, *Juglans*, and *Nyssa*. Benson (1962) lists *A. rhombifolia* and *A. oblongifolia* as vicariants in the California and Southwestern Oak Woodlands and Chaparral, respectively. He feels that the Southwestern Oak Woodlands and Chaparral have been "relatively little modified from the Oligocene prototype, which also had summer rain," these two regions apparently being separated by intervening arid lands by the Pliocene.

The antiquity of the temperate flora of Mexico and Central America has been a subject of dispute among various workers. An excellent review of this problem was made by Rzedowski in 1965.

One view holds that "the present temperate flora of Mexico must have come from the north during the late Pleistocene" because prior to the Pliocene "there was little continuous area with sufficient elevation to support a temperate vegetation . . ." (Sharp, 1953b). Dressler (1954), however, after reviewing the paleobotanical and physiographic evidence, concludes that the temperate types were introduced from the western part of North America as early as the Miocene and reached Guatemala by the Pliocene, the eastern North American plants probably not migrating into Mexico until the early Pleistocene. Chaney (1936), in discussing the movement of temperate forests southward during the cooling period of the Cenozoic states that "a modified type of Miocene forest had migrated as far south as southern Guatemala . . ." by this time, including such genera as *Alnus*, *Arbutus*, *Crataegus*, *Ostrya*, *Pinus*, *Quercus*, and *Salix*. Axelrod (1939) lists the genera *Quercus*, *Cornus*, *Ulmus*, and *Juglans* in Mexico as possibly having differentiated in that area and thus having "no floristic relationship to the northern species of the same genera." McVaugh (1952) states that "such genera as *Alnus*, *Arbutus*, *Carpinus*, and others have persisted in Mexico and adjacent Central America since early Tertiary or even since Cretaceous time . . .". *Alnus rubra*, *A. rhombifolia*, and *A. oblongifolia* all show strong affinities to the species of Latin America and may be remnants of stocks which either did not migrate further south originally, or which originated from a northward-moving Madro-Tertiary flora during or before the Pliocene.

Little is known of the history of the Latin American species of *Alnus* due to the scanty fossil record. All of the taxa are very closely related, and they are not strongly differentiated, indicating relatively recent speciation. Numerical analysis (Furlow, in preparation) indicates the most primitive present segment of the complex to be the population of *A. acuminata* ssp. *arguta* in southwestern Mexico. *Alnus jorullensis*, as well as the other subspecies of *A. acuminata* appear to have diverged primarily in response to differing climates at various altitudes.

ECOLOGY

Most of the alders are associated with wet habitats. The plants may occur in standing water, on stream banks, on wet floodplains, in bogs and muskegs, or on moist mountain slopes. A few are

adapted to somewhat drier conditions. *Alnus viridis* ssp. *crispa*, for example, is found sometimes in apparently dry woods, and *A. jorullensis* often occurs on mountain slopes away from standing or running water. In both of these species, however, the plants are nevertheless usually associated with some source of moisture, even though it may not be as obvious as in the other species. Most alders grow only in full sunlight, an exception again being *A. viridis* ssp. *crispa*, which may occur as an understory component in conifer woods. Where this is the case, the forest is usually very open, and the alder stratum may actually represent a declining successional stage. Nearly all of the taxa are isolated by habitat where their geographical distributions overlap, although some have fairly wide tolerances and may actually occur sympatrically.

All species of *Alnus* are mycotrophic, with root nodules (Figure 1) containing nitrogen-fixing microorganisms (cf. Bond, 1956, 1963; Bond *et al.*, 1954; Hawker & Fraymouth, 1951). That nitrogen-fixation actually occurs has been established by chemical means for *Alnus viridis* ssp. *crispa* (Dalton & Naylor, 1975), and, in a recent paper, Fleschner *et al.* (1976) have measured the rate of nitrogen-fixation in *Alnus incana* ssp. *tenuifolia*. The exact identity of the endophytes has been a matter of dispute since early in the nineteenth century (cf. Kelley, 1950). Whatever their identity, there is evidence (Bond, 1963; Rodriguez-Barrueco & Bond, 1968) that the nitrogen-fixing endophytes of *Alnus* are specific for the species upon which they are growing.

Symbionts forming mycorrhizae on *Alnus* have also been reported (Masui, 1926; Klečka & Vukalov, 1935; Trappe, 1964; Neal *et al.*, 1968). These organisms apparently have a role in nutrient absorption and the minimization of root diseases, but their biology is not yet well understood.

The role of *Alnus* in plant succession has been studied by a number of investigators, especially in areas recently deglaciated in southern Alaska. In studies at Glacier Bay, Cooper (1923a, 1923b, 1931, & 1939) showed that *Alnus* plays an important part in the succession of recently deglaciated land. He demonstrated that from a pioneer stage of mosses, horsetails, *Epilobum*, and *Dryas*, the community moves through a thicket stage of willows and alders before reaching the forest climax of spruce. This work has been continued by Crocker and Major (1955), Crocker and Dickson (1957), Lawrence (1958), Heilman (1966), Mitchell (1968), Ugolini

(1968), Hurd (1971), Reiners *et al.* (1971), and others. Reiners *et al.* (1971) estimate the length of stages in the successional sere at Glacier Bay as follows: horsetails, sedges, *Epilobium*, *Salix*, and *Populus*, 0 to 5 years; *Dryas*, 5 to 20 years; *Alnus viridis* ssp. *sinuata*, 20 to 40 years; *Populus* and *Picea sitchensis*, 50 to 70 years; *Picea sitchensis* forest, 75 to 100 years; and *Tsuga* forest, over 100 years. One of the roles of *Alnus* may be the addition of nitrogen to the soil. Lawrence (1958) found that nitrogen entering the soil originates mainly from the dropped leaves rather than from the nodules themselves. He showed that the autumn foliage of *Alnus viridis* ssp. *sinuata* contains up to 3% (dry weight) combined nitrogen and estimated that an alder thicket five years old and five feet tall adds 140 pounds of nitrogen to the soil per acre per year from the fallen leaves. Crocker and Dickson (1957) found that the soil in alder thickets had accumulated over one ton of nitrogen per acre by the end of 70 years. Another study, by Dalton and Naylor (1975), showed insignificant nitrogen accumulation in soil containing plants of *Alnus viridis* ssp. *crispa*, though these workers apparently failed to consider fallen leaves as a possible source of the nitrogen.

Crocker and Major (1955) found that the soil in alder thickets can change in pH from values over 8.0 to less than 5.0 within 35 to 50 years. In this period, organic matter (with a pH of 4.2 to 4.6) six to seven centimeters deep had accumulated below the plants. The 18-inch deep mineral soil profile and forest floor combined had accumulated almost 4.0 kilograms of organic carbon per square meter.

Other species of *Alnus* cited by authors as pioneers in succession include *Alnus rubra* in the Pacific Northwest (Worthington *et al.*, 1962; Newton *et al.*, 1968) and *A. acuminata* ssp. *arguta* in southern Mexico and in Guatemala (Standley & Steyermark, 1952). From information on the labels of herbarium specimens used in this study, it appears that virtually every species plays this role, occurring regularly on cut or burned-over land and in abandoned fields. Many species (*A. incana* ssp. *rugosa*, *A. serrulata*, *A. viridis* ssp. *crispa*) are regarded as weeds, growing in ditches, along embankments, on pond shores, in wet pastures, and other places where they are not desired.

In some cases where *Alnus* might be expected as an important pioneer in succession, it is absent. Tisdale *et al.* (1966) point out that

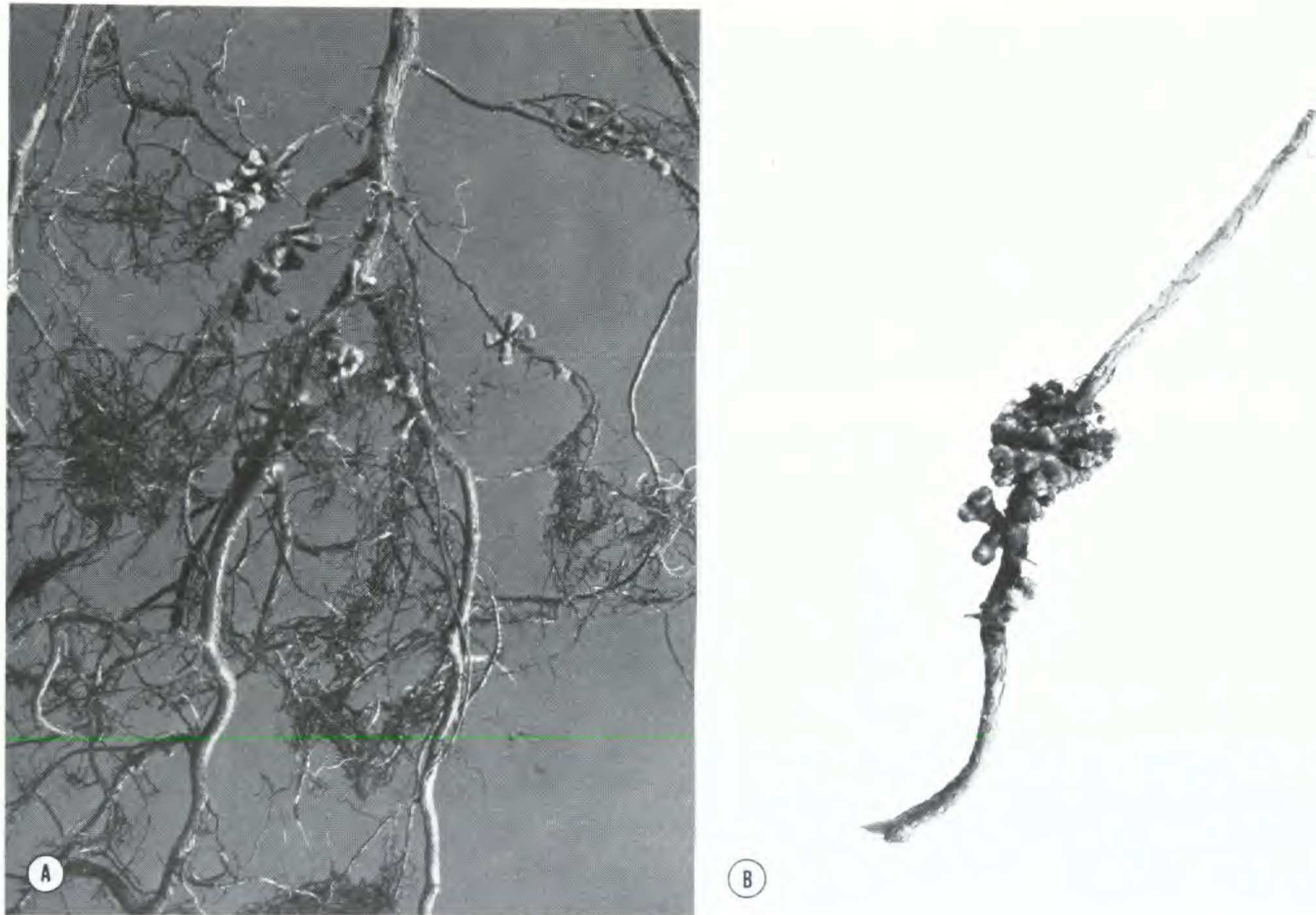


Figure 1. Nodules of nitrogen-fixing endophytes on roots of *Alnus serrulata*. A, $\times 0.7$. B, $\times 1.5$.

alders are not present in the successional vegetation occurring on recently glaciated land on Mt. Robson in the Canadian Rocky Mountains even though the environmental conditions seem to be favorable for its development there. Additional study will be necessary for a more complete understanding of this problem as well as the general role of these plants in succession.

McVean, in a series of papers on the ecology of *Alnus glutinosa* in England (1953a, 1953b, 1955, 1956a, & 1956b) makes a number of observations that also appear to be true for the American species. Among these is the fact that the root system has both surface and deep branches, enabling the plant to survive in either waterlogged soil or where the water table is deeper. Only the surface roots bear nodules, however. He also shows that seed germination is independent of light, normal temperature variation, and pH within the range of 3.5 to 8.0, but is sensitive to low oxygen and moisture levels. He (1953a) lists a large number of animal feeders, parasites, insect pests, and destructive fungi and discusses the effects of each on plants in various stages of their life histories.

MORPHOLOGY AND ANATOMY

Habit. Members of the genus *Alnus* are woody plants ranging in size from small shrubs to large trees. In general, the species of warm climates are arborescent while those of cool-temperate, boreal, and montane regions are fruticose in form. Two American shrubby species (*Alnus maritima* and *A. incana*) approach tree stature. Even those species which normally attain the size of trees usually possess several main trunks, pointing, perhaps, to a shrubby ancestral habit. The fruticose form in modern taxa, however, is regarded as an adaptation to cool climates which has arisen from the tree habit independently in a number of lines. Photographs showing the habits of representative taxa are provided in Figures 2 and 3.

Stems. Mature stems in *Alnus* range in diameter from about one centimeter to more than two meters. In most species the bark is smooth, though in larger trees it is sometimes broken into flat plates or can be furrowed and corky (Figure 4). All of the Latin American taxa develop transverse constrictions, as shown in Figure 4. It is unknown whether this feature is caused by external environmental factors. On smooth bark, the lenticels are visible and range from very

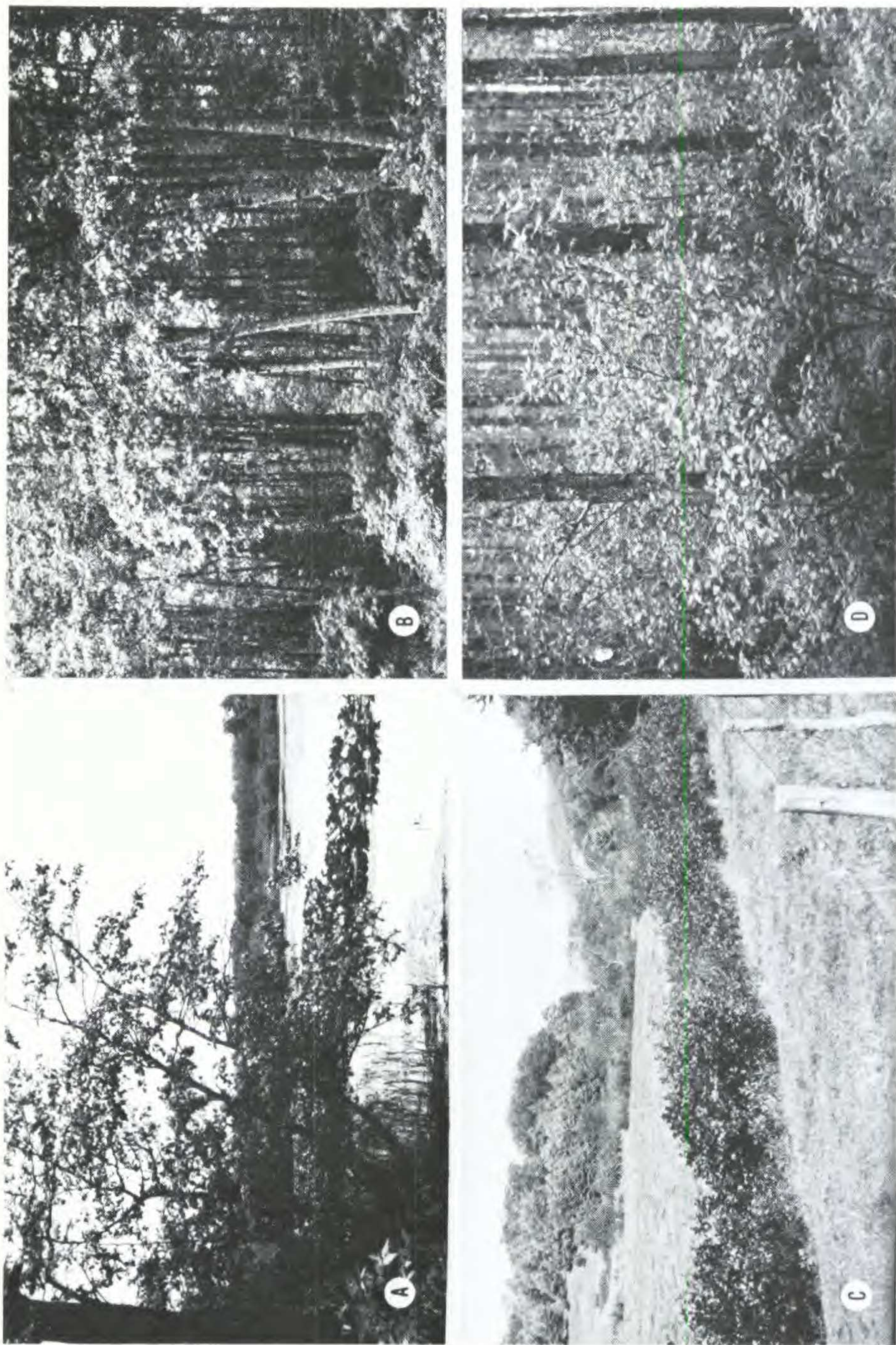
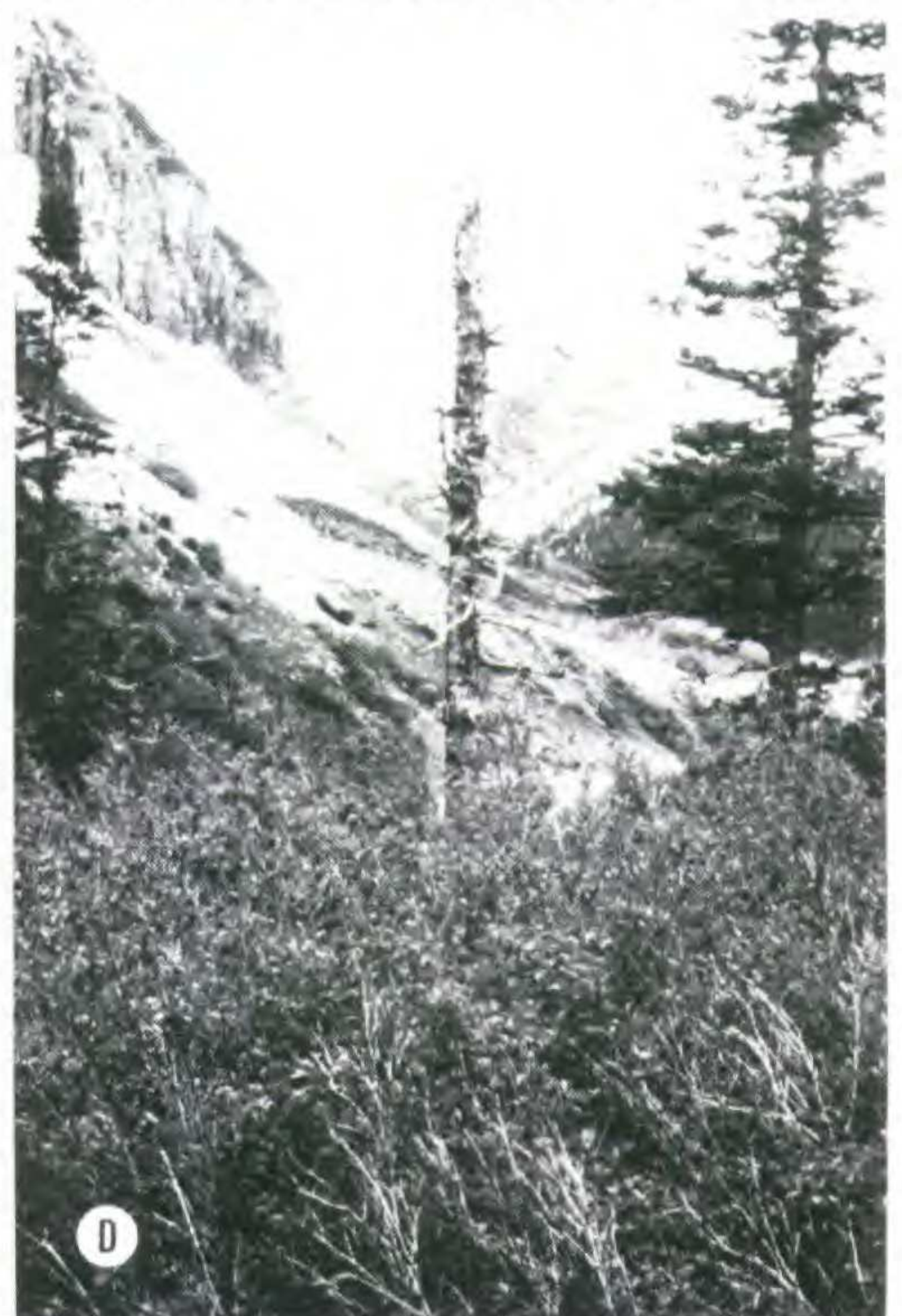


Figure 2. Habits and habitats of representative species of *Alnus*. A, *Alnus incana* ssp. *rugosa*, large shrub on the bank of the Pigeon River in northern Indiana. B, *A. rubra*, medium-sized trees forming a dense stand on a river floodplain in west-central Washington. C, *A. serrulata*, medium-sized shrubs growing on the banks of a small stream in the Blue Ridge Mountains of southern Virginia. D, *A. viridis* ssp. *crispa*, medium-sized shrubs forming an understory in pine woods in central Alberta.



small and inconspicuous round spots (e.g., *A. serrulata* and *A. maritima*) to large, prominent, transverse markings (e.g., *A. incana* ssp. *rugosa*). The presence of smooth bark in the shrubby species, as well as the shrub habit itself, may be a result of neoteny, these species never reaching "maturity" in an anatomical sense (Hall, 1952).

The twigs are terete, but in cross-section have a triangular-shaped region of pith in the center which varies in form from that of a symmetrical (equilateral) triangle in *Alnus maritima* and *A. rhombifolia* to nearly linear in *A. viridis* ssp. *crispa*. In *A. incana* and *A. serrulata*, the pith is equilaterally-triangular, but with strongly concave sides. The color ranges from a light buff in *A. viridis* and *A. rhombifolia* to a dark brown in *A. incana*, *A. serrulata*, and *A. acuminata*. Sometimes pronounced longitudinal ridges are evident on the surface of the twigs, especially in *Alnus acuminata* and *A. maritima*. In transection these ridges are seen to contain air chambers.

The epidermis of young shoots is usually somewhat pubescent, glandular, and resin-coated. The pubescence and glands vary in density, color, and size, but are otherwise similar from species to species. The glands are invariably denser and larger at the nodes than along the internodes of the stems. On the youngest twigs, the lenticels are always oriented longitudinally, but these rapidly become laterally elongate with secondary growth of the stem. The leaf scars are triangular and about as high as broad. They bear five bundle scars, the upper two much larger than the lower three, which may be fused together. In *Alnus rhombifolia*, *A. acuminata*, *A. rubra*, and *A. jorullensis* the lower two lateral bundle scars are more elongate than those of the other species, although this feature varies from specimen to specimen.

In *Alnus viridis* one can usually see a differentiation in the length of the twigs. The leaves are borne on short spur shoots growing laterally on longer branches. In other species the leaves are borne directly on the long shoots. After one to several seasons, the short shoots may elongate and become long branches.

Figure 3. Habits and habitats of representative species of *Alnus*. A, *Alnus oblongifolia*, trees ca. 17 m tall in a stream on Mt. Graham in southern Arizona. B, *A. jorullensis* ssp. *jorullensis*, tree ca. 10 m tall on Volcan Popocatepetl, Mexico. C, *A. rhombifolia*, trees ca. 4 m tall on the banks of the Trinity River in northern California. D, *A. viridis* ssp. *sinuata*, shrubs ca. 2.5 m tall covering a subalpine mountainside in Glacier National Park, Montana.

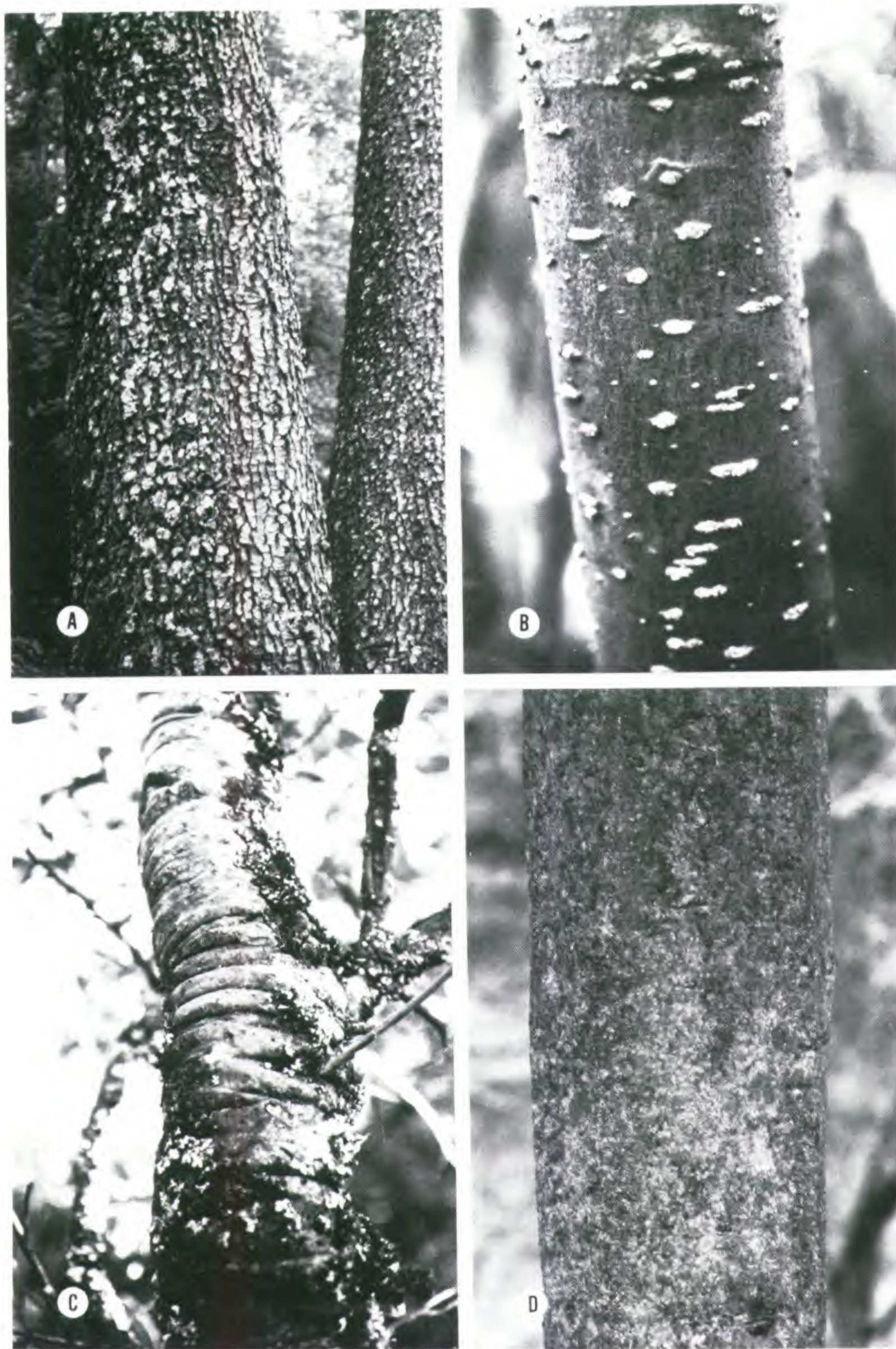


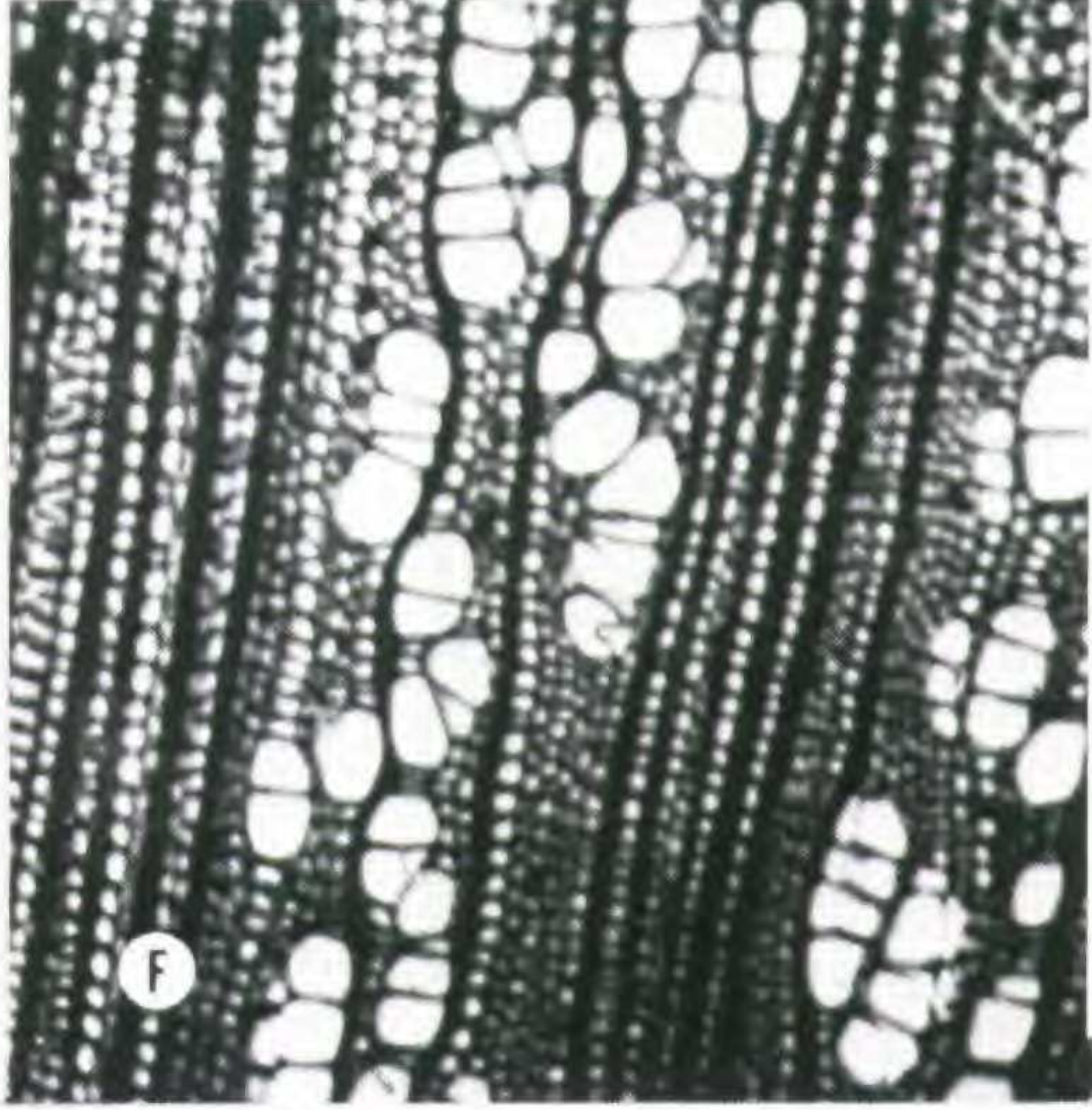
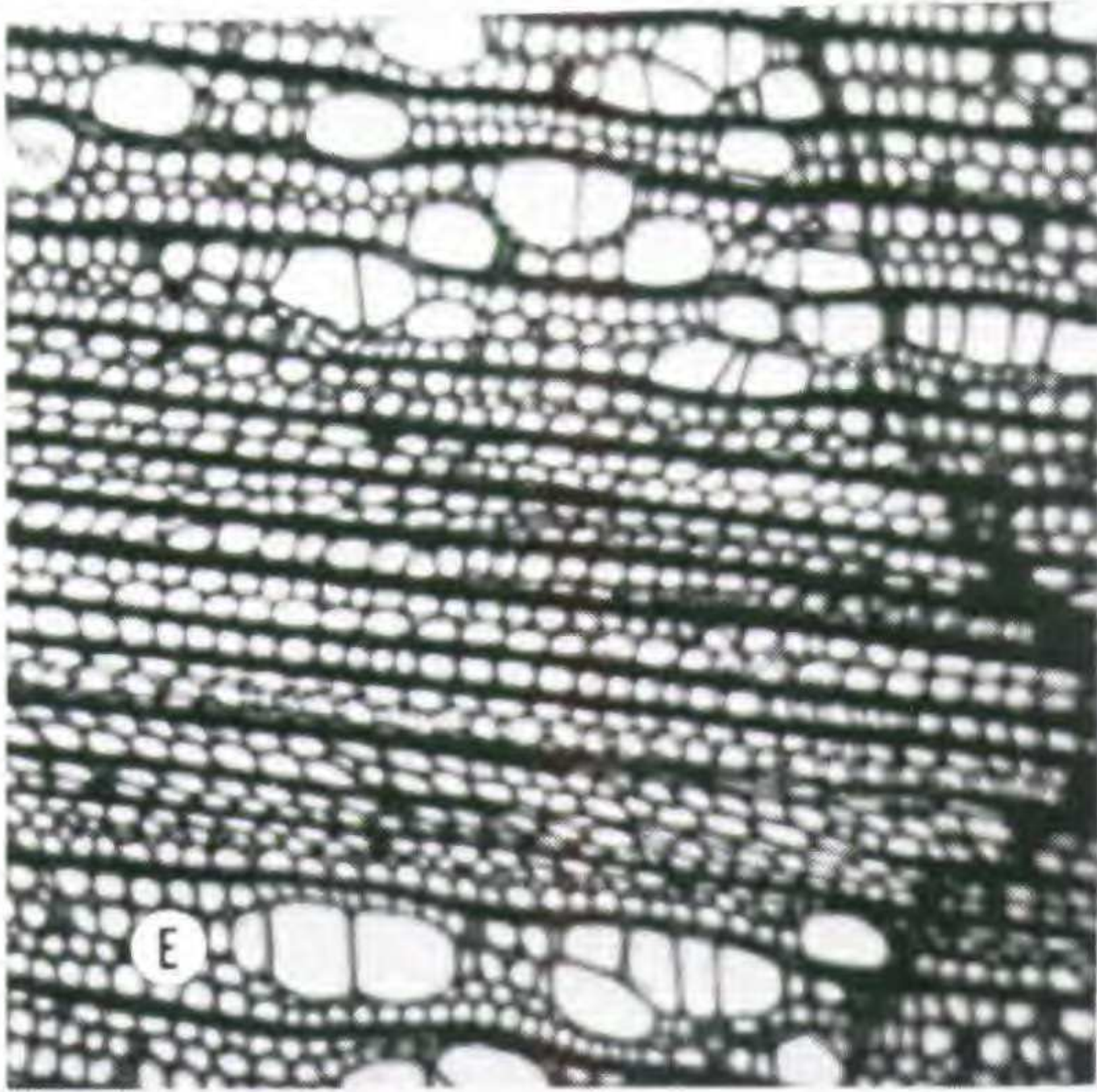
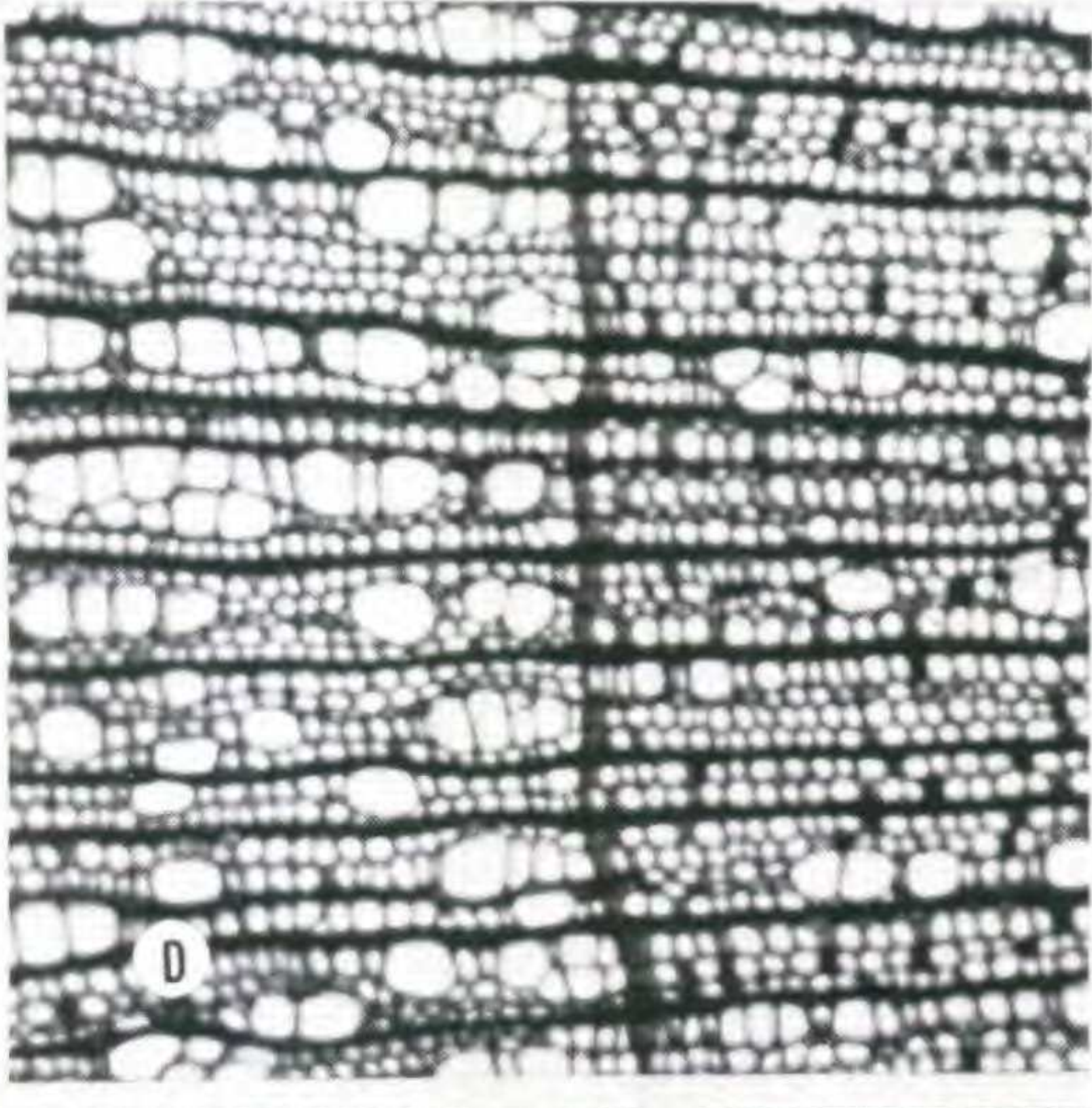
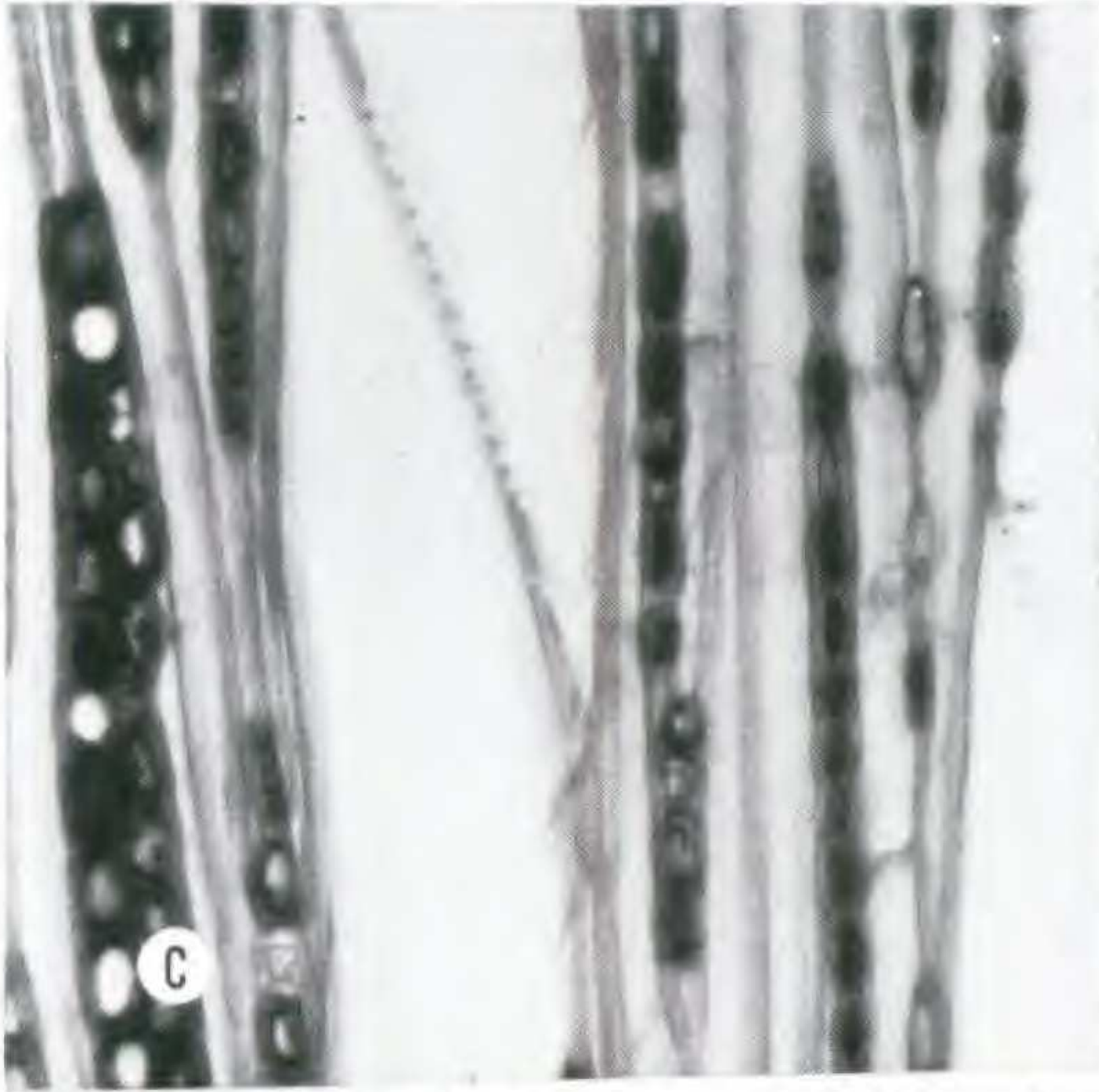
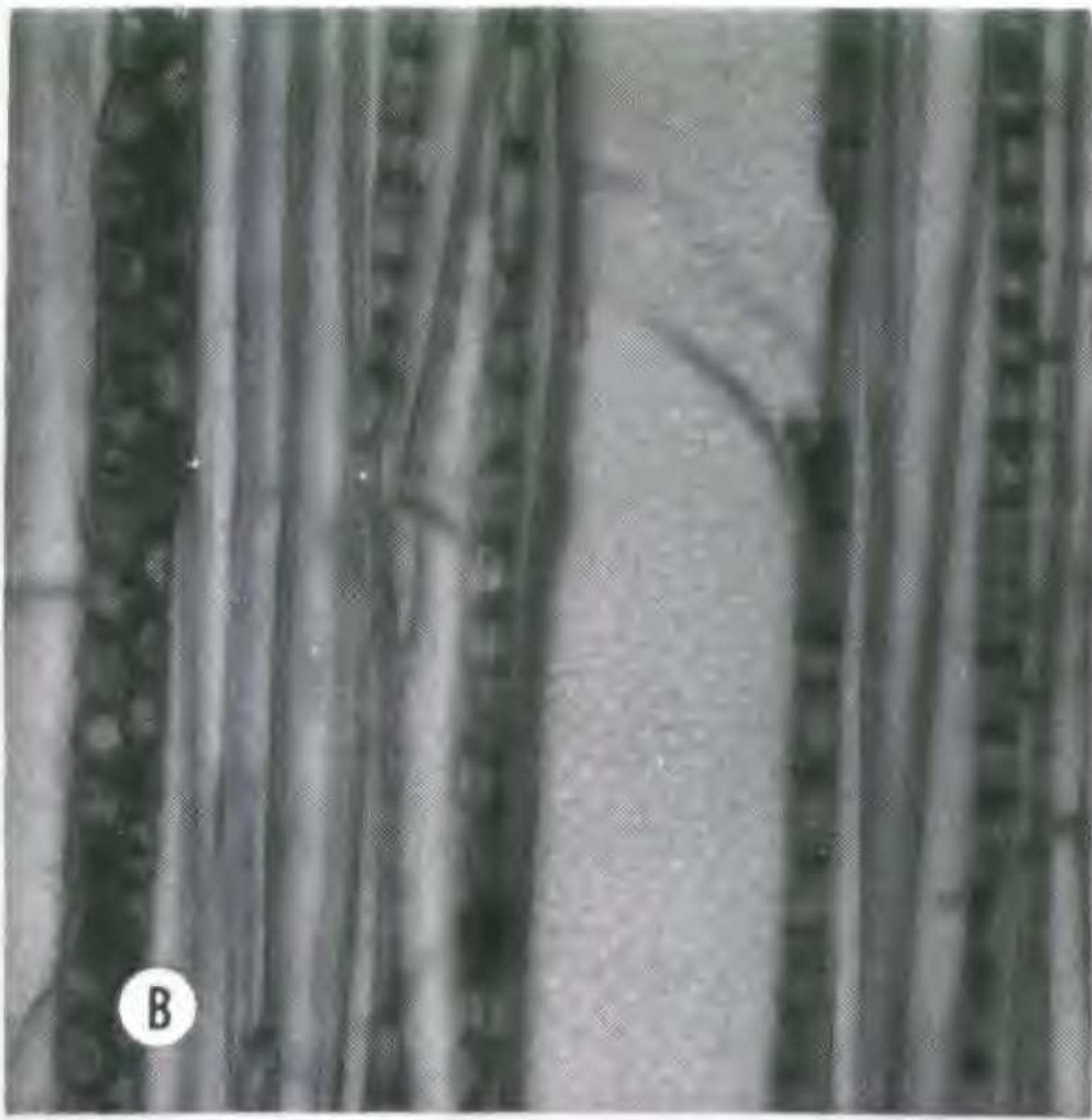
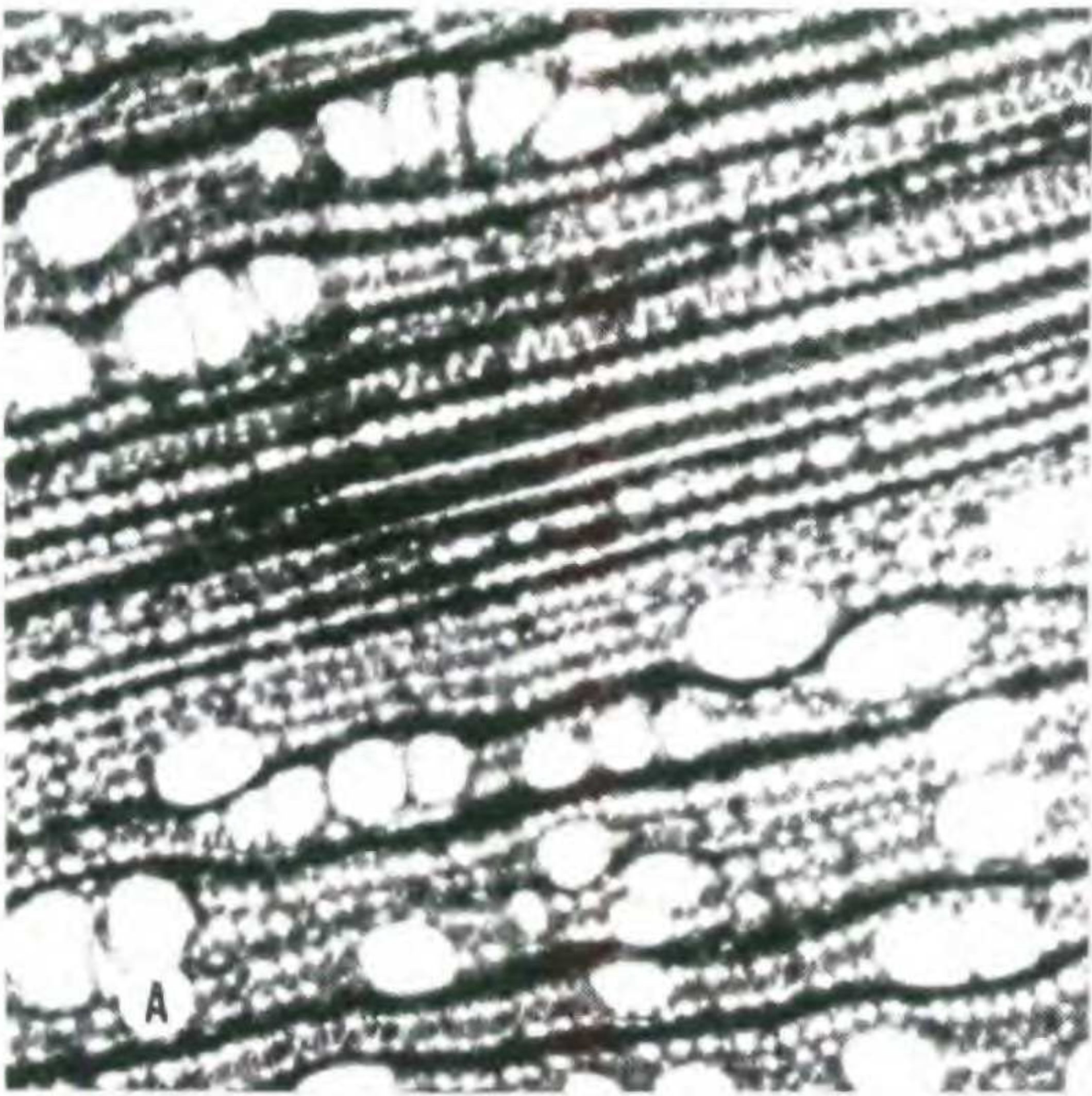
Figure 4. Bark of a representative species of *Alnus*. A, *Alnus oblongifolia*, $\times 0.03$. B, *A. incana* ssp. *rugosa*, $\times 0.2$. C, *A. jorullensis* ssp. *jorullensis*, $\times 0.17$. D, *A. serrulata*, $\times 0.33$.

The wood of *Alnus* has long interested plant anatomists. Bailey (1911) first showed a phylogenetic series involving the building up of large multiseriate rays from uniseriate ones. He noted that there is no inclination of any aggregation in *A. incana*, *A. rubra*, and *A. maritima*. *Alnus rhombifolia* was shown to have completely fused aggregate or compound rays. In a second paper (Bailey, 1912) he discusses in detail the evolution of the compound ray and shows a reversal in the trend (from multiseriate to uniseriate) in several species, including *A. viridis* ssp. *crispa* and "*A. acuminata*". This phenomenon has also been discussed by Hoar (1916), Forsaith (1920), Anderson and Abbe (1934), and Hall (1952). The latter states that aggregate rays are absent in *A. oblongifolia*, *A. jorullensis*, *A. ferruginea*, and *A. mirbelii*.

All of the above authors describe the wood of "*Alnus acuminata*" as having uniseriate rays, and several of them note that growth rings are absent in this species. It is not certain, however, that *A. acuminata* of South America is what these workers actually had in mind. In each case, anatomical material apparently was obtained from cultivated plants, although the authors are not clear on this point. Examination of wood of all the species showed that multiseriate rays are present in all of them except *A. viridis*, which does, in fact, have uniseriate or partly biseriate rays. Some species, such as *A. incana* ssp. *rugosa*, *A. serrulata*, and *A. maritima*, possess rather poorly-developed multiseriate rays, however (Figures 5 & 6). All species have uniseriate rays between the multiseriate ones.

The wood is made up primarily of vessels and fiber tracheids, although some true tracheids may be present in certain species. The outer part of the primary cortex is always collenchymatous (Metcalf & Chalk, 1950). The pericycle contains a composite and continuous ring of sclerenchyma, and the secondary phloem contains stone cells. The cork cells are almost tabular in shape.

Hall (1952), in characterizing the family Betulaceae, its tribes, and its genera on the basis of wood anatomical features, provides the most complete description of *Alnus* wood available. Species differences are shown to occur with respect to vessel length, diameter, frequency, shape in cross-section, and the number of bars in the scalariform perforation plates. Both tracheids and fiber tracheids are present in some species, while only fiber tracheids occur in others. Intervascular pitting may be opposite, alternate, or transitional, depending on the species.

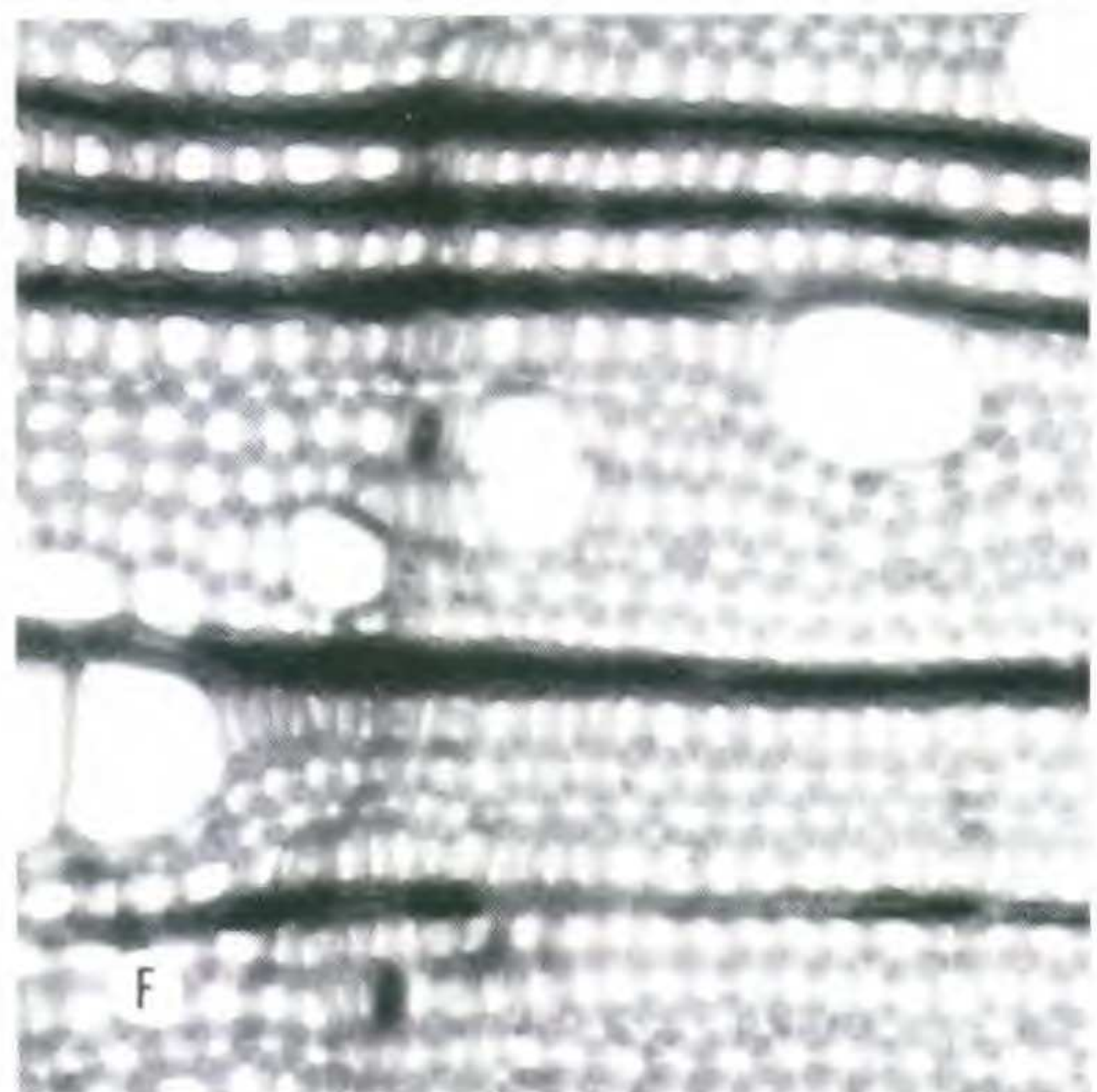
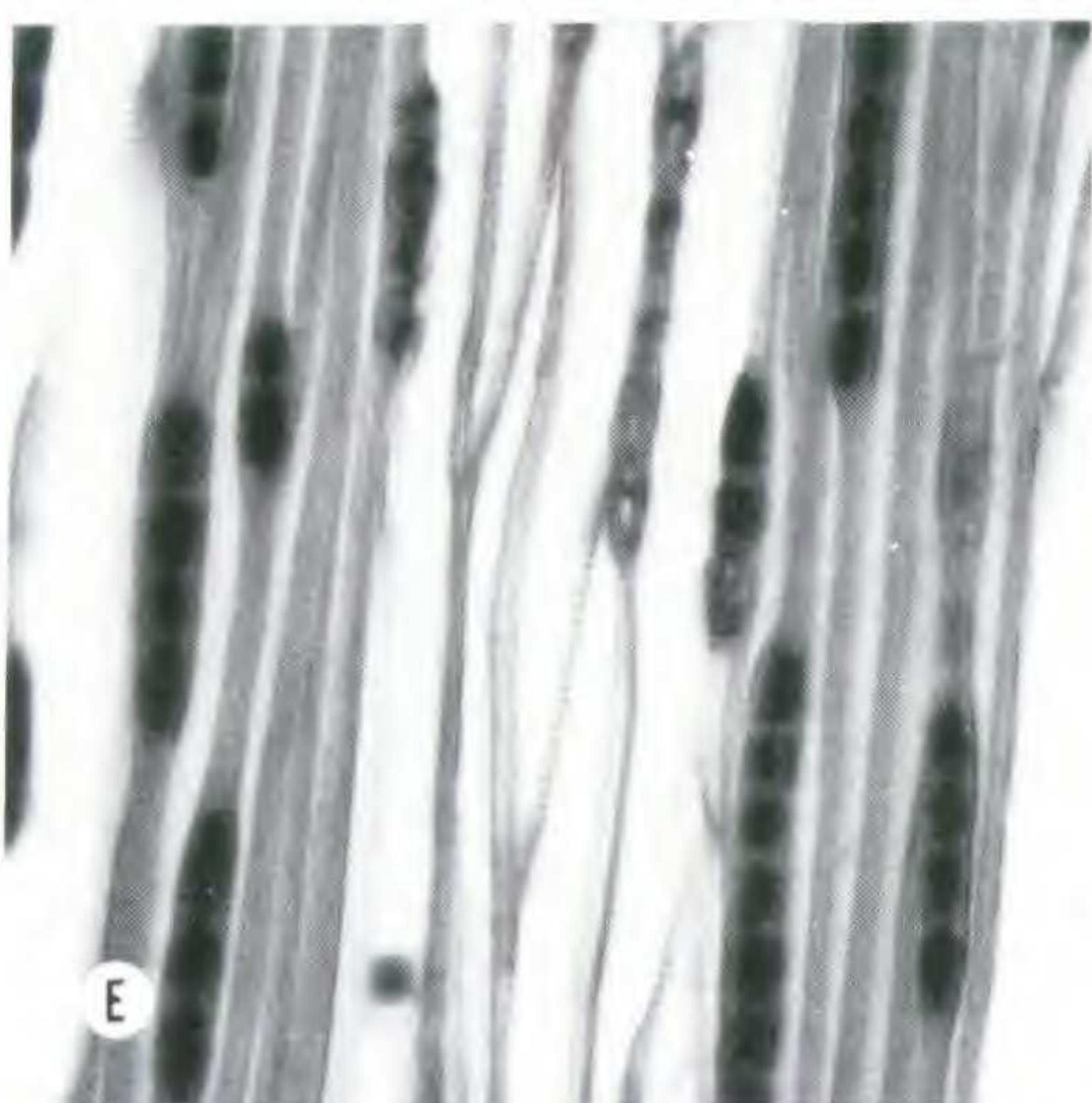
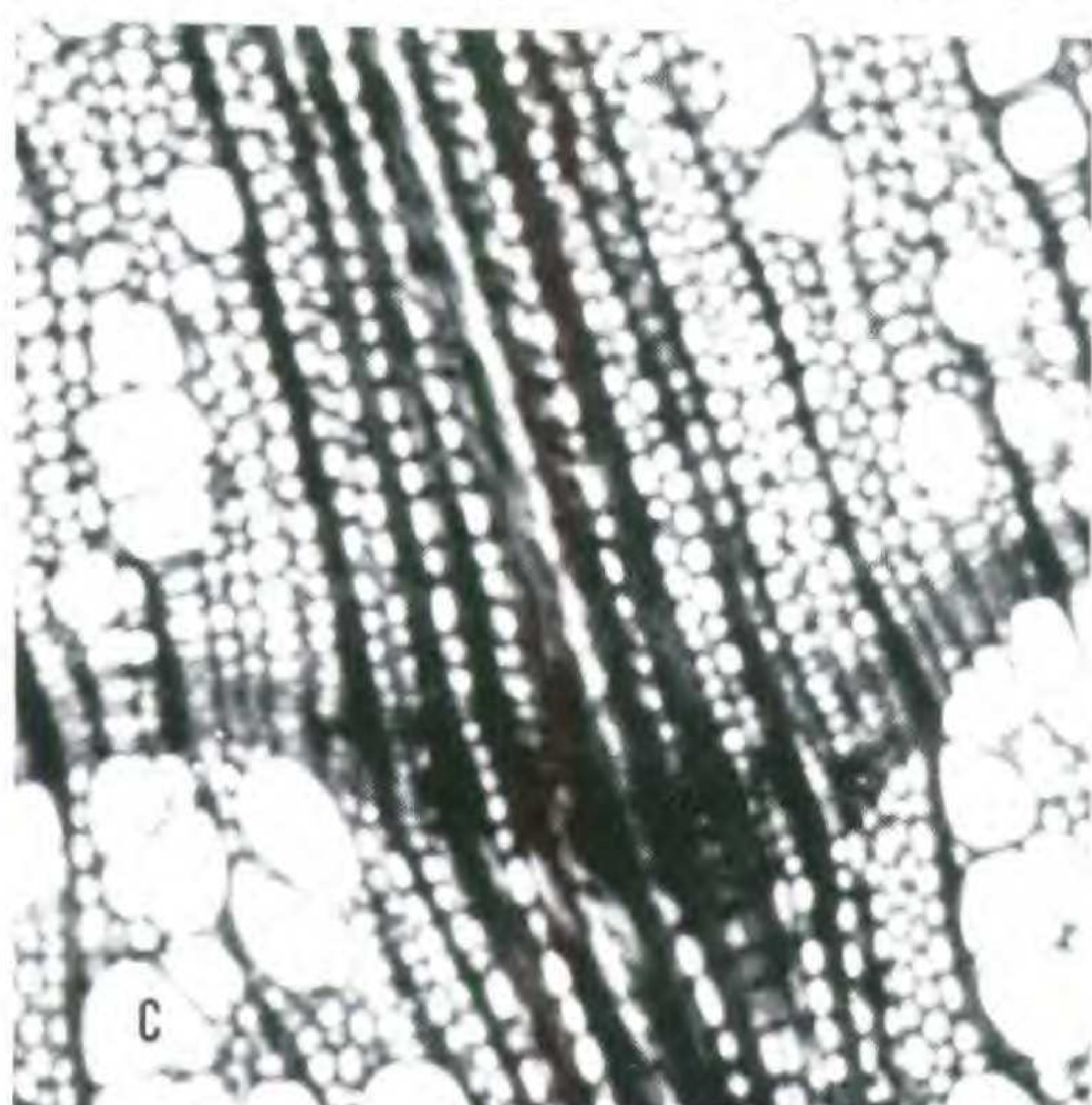
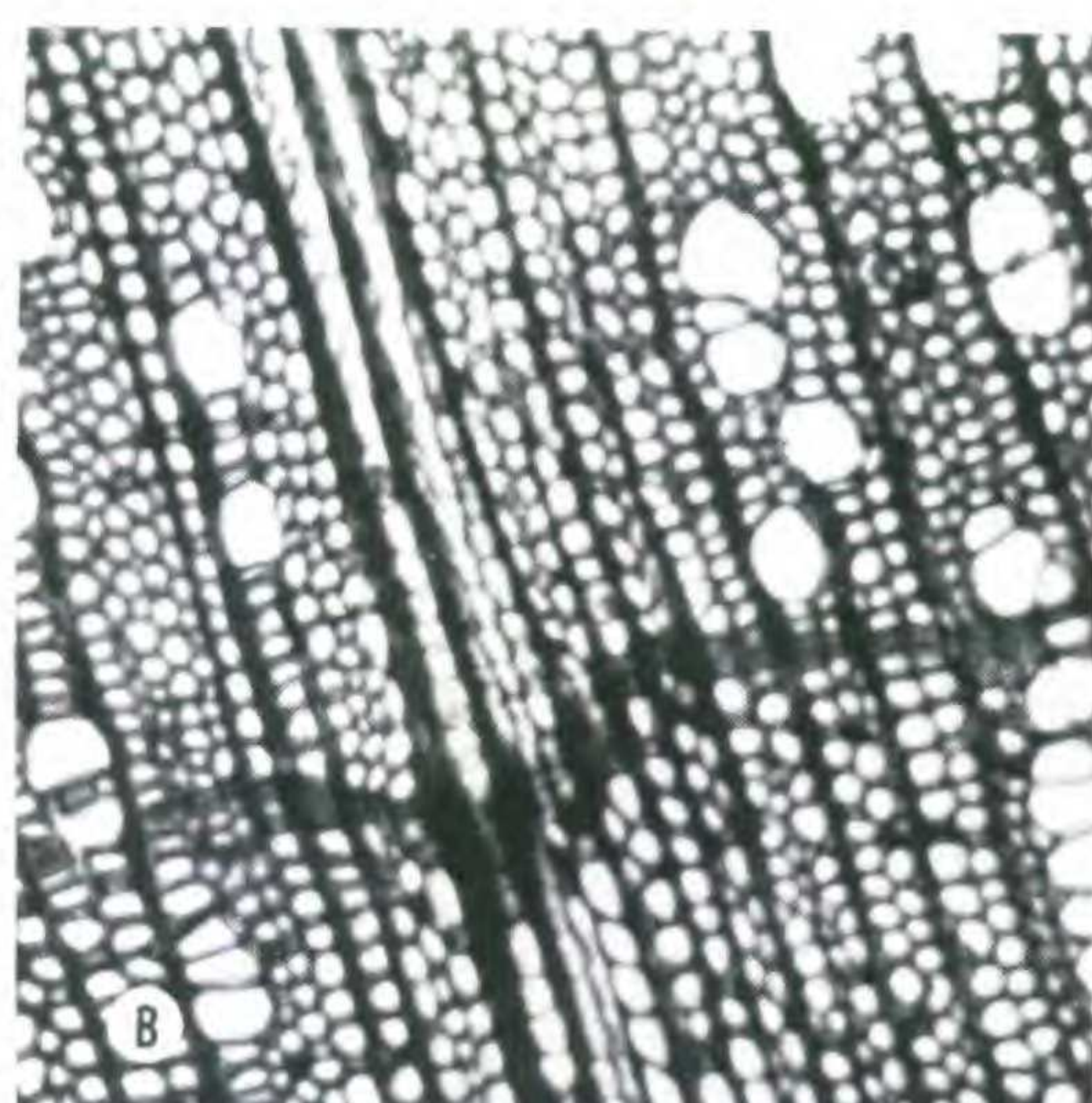
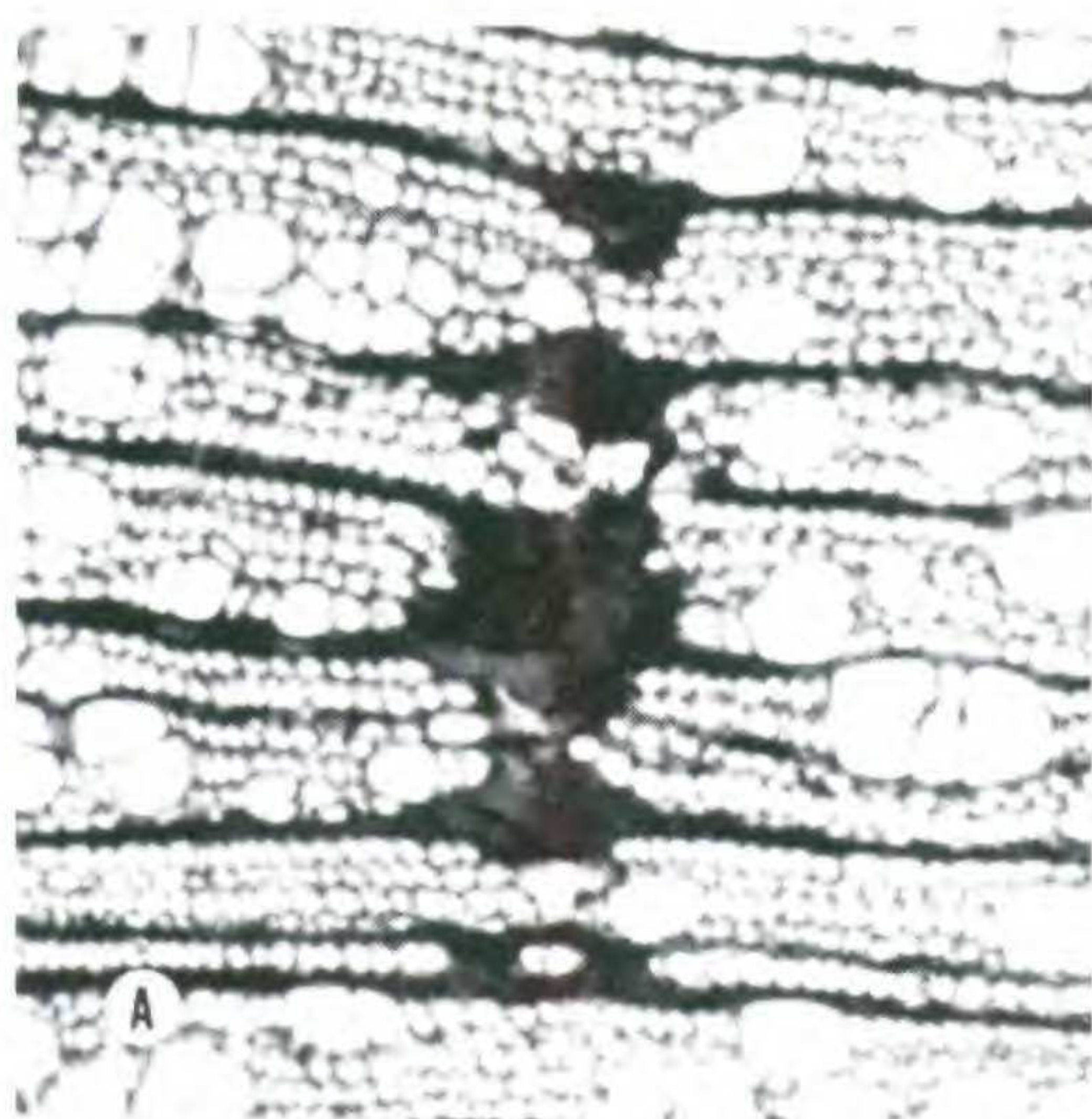


Specialized features, according to Hall (1952), include alternate intervacular pitting, as opposed to opposite; a large or small number of bars in the perforation plates rather than an intermediate number; the absence of true tracheids; and uniseriate rays by reduction from aggregate rays. Other features in an advanced state include a reduced frequency of vessels, angular vessel shape in cross section, and a large number of vessels per cluster. Unfortunately, Hall did not examine fossil alder wood in the collection of his data. Such a study might have proved useful in the determination of primitive and advanced conditions in wood traits.

Many of the species names used by Hall are of uncertain application, and he does not include documentation of the specimens studied. In addition, in many cases he does not name the species showing the particular features discussed, so his work is of limited value at the species level. From the information available, however, and from my own observations, it is possible to make the following general statements.

The wood of *Alnus viridis* is specialized in that it possesses uniseriate rays apparently derived from multiseriate ones by reduction and a relatively large number of vessels per unit area. It is primitive, however, in that the vessels are small and intervacular pitting is opposite. The wood of *A. incana* and *A. serrulata* is somewhat advanced in that it possesses moderate-sized vessels of intermediate frequency and with alternate intervacular pitting, but it is primitive in that it has only moderately well-developed multiseriate rays. Wood of *A. maritima* is advanced in that its vessels are small and infrequent, but it is primitive in possessing aggregate rays. *Alnus jorullensis* is distinct from the other species in having very angular vessels of medium size. The wood of this species is primitive with respect to its high frequency of vessels and its multiseriate rays.

Figure 5. Photomicrographs of *Alnus* wood. A, *Alnus acuminata* ssp. *arguta*, transverse section showing aggregate rays and large diameter vessels, $\times 107$. B, *A. acuminata* ssp. *arguta*, tangential section showing rays and details of the vessel wall, $\times 263$. C, *A. acuminata* ssp. *glabrata*, tangential section showing uniseriate and biseriate rays and details of the perforation plate of a vessel, $\times 263$. D, *A. incana* ssp. *rugosa*, transverse section showing little tendency for aggregation of the rays, $\times 107$. E, *A. incana* ssp. *tenuifolia*, transverse section showing aggregation of rays and moderate diameter vessels, $\times 107$. F, *A. jorullensis* ssp. *lutea*, transverse section showing multiseriate rays, $\times 107$.



Wood of *A. rhombifolia*, *A. oblongifolia*, and *A. acuminata* is generally primitive in having aggregate rays, but advanced in showing numerous, large, circular vessels. Thus, each species can be seen as specialized in some wood features and not in others, probably in response to the particular environmental conditions present in its habitat.

Stipules. The stipules vary greatly in size, ranging from about 4 to 15 mm in length and from about 0.5 to 6 mm in width, as shown in Figure 7. *Alnus viridis*, *A. serrulata*, and *A. acuminata* possess relatively large stipules, while *A. maritima* and *A. oblongifolia* have much smaller ones, being particularly reduced in width. Mostly, they are ovate in shape with acute tips. Like the leaves, they are pubescent and glandular on the abaxial surface. The margins are lined with longer and coarser hairs than those borne on the surface.

Winter Buds. The buds of *Alnus* are stalked (though nearly sessile in *A. viridis*). The bud stalks are very short modified branches, often with one or more nodes which bear reduced leaves as the buds are forming. In all of the species except *A. viridis* the buds are protected by two slightly modified stipules and sometimes one or more of the stipules of the next level of the bud (Figures 8 & 9). These may cover the entire bud or be reduced in size or entirely absent (*A. maritima* and *A. oblongifolia*). The stipular scales are equal in size, and when large enough, valvate. Buds of *Alnus viridis* are covered by several unequal bud scales apparently derived from stipules. In all species the stalks and scales are pubescent, glandular, and covered with resinous secretions. Within the buds the leaves are conduplicate and usually more or less plicate within their stipules. However, the degree of development of the young leaves varies considerably in different species.

Figure 6. Photomicrographs of *Alnus* wood. A, *Alnus jorullensis* ssp. *lutea*, transverse section showing "wax chambers", $\times 107$. B, *A. maritima*, transverse section showing small-diameter vessels and a small multiseriate ray, $\times 107$. C, *A. rhombifolia*, transverse section showing a well-developed multiseriate ray, $\times 107$. D, *A. viridis* ssp. *crispa*, transverse section showing small-diameter vessels and uniseriate rays, $\times 107$. E, *A. viridis* ssp. *crispa*, tangential section showing the vertical nature of the rays, $\times 263$. F, *A. viridis* ssp. *sinuata*, transverse section showing slight aggregation of the rays, $\times 263$.



Figure 7. Stipules and expanding leaves of representative species of *Alnus*, all $\times 1.0$. A, *Alnus incana* ssp. *rugosa*. B, *A. maritima*. C, *A. rhombifolia*. D, *A. viridis* ssp. *crispa*.



Figure 8. Twigs with winter buds of representative species of *Alnus*. A, *Alnus oblongifolia*. B, *A. maritima*. C, *A. rubra*. D, *A. serrulata*.

Leaves. The leaves of *Alnus* are borne alternately along the twigs. The petioles are terete and are usually rather deeply grooved above. The leaves are typically ovate and double-serrate. However, *Alnus maritima* and other members of subg. *Clethropsis* have much narrower leaves with low, distant, upturned, single teeth (though the leaves of seedlings of *A. maritima* may sometimes be ovate and double-serrate). Many species in the genus have laciniate forms (cf. Hylander, 1957). In North America, local populations of *A. incana* ssp. *rugosa*, *A. viridis* ssp. *sinuata*, and *A. rubra* demonstrate this condition. Several species, including *A. maritima*, *A. serrulata*, and *A. jorullensis*, have obovate leaves, apparently derived from the ovate form by suppression of linear development accompanied by increased lateral growth in the apical region. The range of variation in shape and margin for each American taxon is shown in the series of leaf outlines pictured in Figures 10, 11, and 12.

The leaves are pinnately veined, the lateral veins sometimes branching one or two additional times to form subsecondaries near the margins, especially toward the base. Venation in *Alnus maritima* is semicraspedodromous to eucamptodromous, while in all the other species it is simply-craspedodromous (cf. Hickey, 1973). The size of the leaf is not correlated with the number of lateral veins but with their distance from each other. The lateral veins of all species form about the same angle with the midrib (30 to 40 degrees). Between the lateral secondary veins are tertiary cross-veins. These are well-developed, forming ladder-like reticulations in some species, but they may be incomplete in others. Within these reticulations are areoles containing simple to branching veinlets.

Leaf margins are somewhat thicker than other parts of the blade, especially at the apices of major teeth, giving them a glandular-tipped appearance. In some species (best illustrated by *Alnus rubra*) the margin is revolute (Figure 13). The base is usually rounded, truncate, or cordate, but it may be extended or even attenuate. The apex is usually acute, but its shape ranges from long-acuminate to truncate to deeply notched in some species (Figures 10, 11, & 12).

The foliage of all the alders is pubescent, especially along the major veins on the abaxial surface, although a few taxa such as *Alnus viridis* ssp. *sinuata* and *A. acuminata* ssp. *glabrata* are essentially glabrous. The hairs are simple, straight, and borne mainly on the veins and veinlets, even in densely-pubescent forms. They vary in length, color, and density, but not in general shape or appearance.

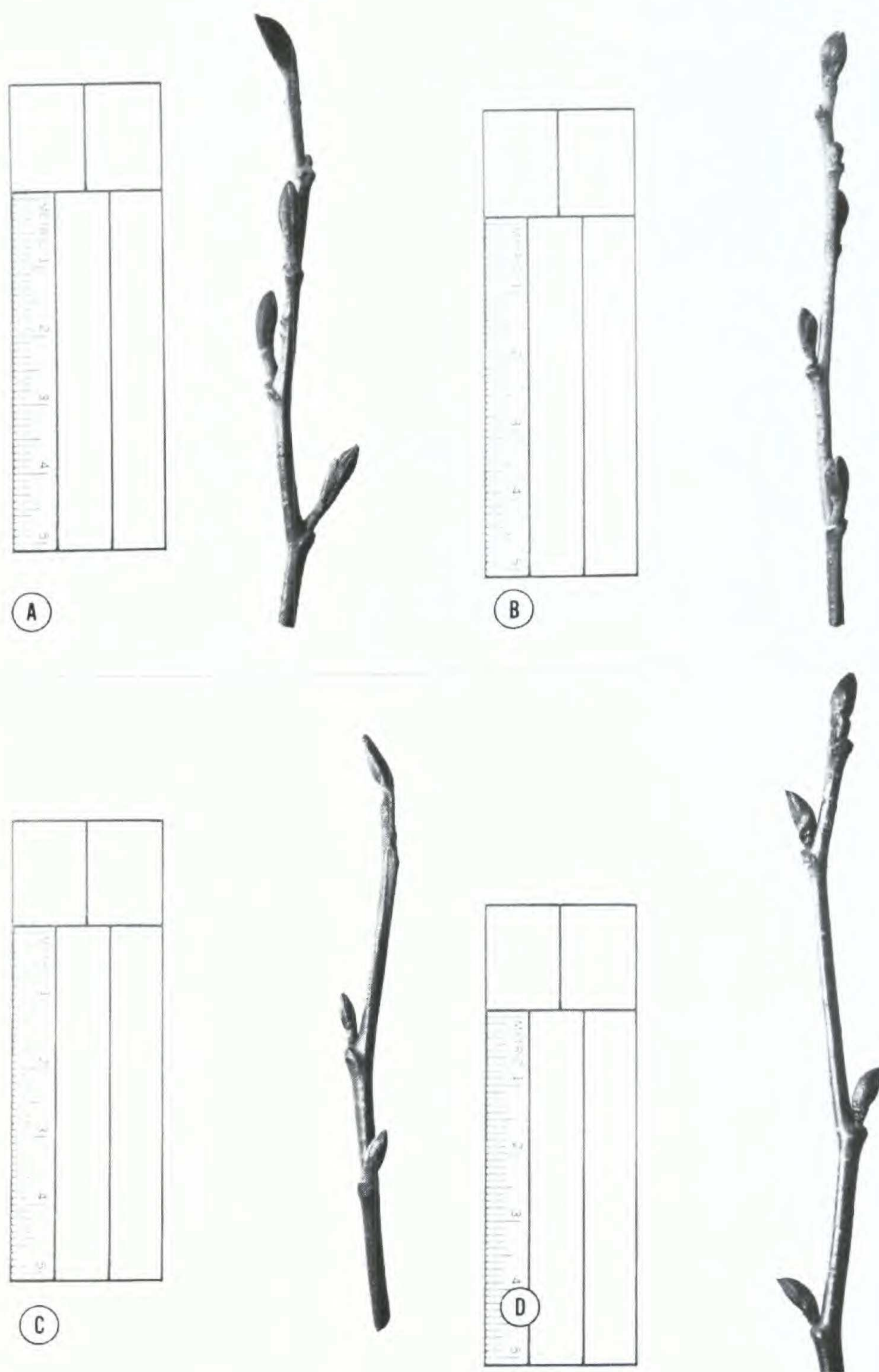


Figure 9. Twigs with winter buds of representative species of *Alnus*. A, *Alnus incana* ssp. *rugosa*. B, *A. incana* ssp. *tenuifolia*. C, *A. rhombifolia*. D, *A. viridis* ssp. *crispa*.

The leaves of all species of *Alnus* are glandular as well as pubescent (Figure 14). The glands, which are more frequent on the lower surface and petiole than above, are described by Metcalf and Chalk (1950) as "consisting of a short but broad stalk composed of low, suberized cells and a shield-like head made up of cells appearing to be polygonal in surface view, but resembling a palisade in sections of the gland." The development of the glands is described by Dorman (1924), who found that they secrete a high molecular weight polyterpene. The glands may be large, yellow, and crowded, as in *Alnus jorullensis* ssp. *lutea*, or they may appear small, dark, and sparse, as in *A. incana* ssp. *rugosa*. They often darken with age, especially on the adaxial surface. The leaves, like the twigs and buds, are often covered with a thick deposit of resinous material, the amount varying from species to species. Of the American species, *A. viridis* is by far the most glutinous.

The anatomy of leaves of the Betulaceae was comprehensively treated by Boubier (1896), who shows that *Alnus* varies considerably in its leaf structure and describes the blade, veins, and petiole histologically (cf. also Solereder, 1908). The stomata are ranunculaceous (surrounded by several irregularly-arranged epidermal cells) and present only on the abaxial surface (Figure 15). A hypodermis is present just below the epidermis in some species, being better developed in some than in others (Boubier, 1896). The hypodermis is found in species of all subgenera.

Inflorescences. *Alnus* is monoecious with the flowers borne in catkins, the staminate pendent and the pistillate erect (Figure 23). The pistillate catkin was shown by Abbe (1935) to be composed of numerous cymules arranged spirally on a primary axis. Each cymule bears three levels of bracts, only the two tertiary florets being present except in rare cases. The staminate catkins are likewise made up of tiny cymules, but all three florets are usually present. *Alnus viridis* and *A. maritima* lack one of the two tertiary bracts of the staminate cymule, while both are usually present in all of the other species.

Alnus maritima and its allies of southern Asia bear the staminate catkins singly in the axils of leaves at the tips of branches and the pistillate catkins singly in leaf axils on the same branch just below the staminate. All of the other species bear the pistillate catkins in racemose clusters just below the solitary and axillary staminate

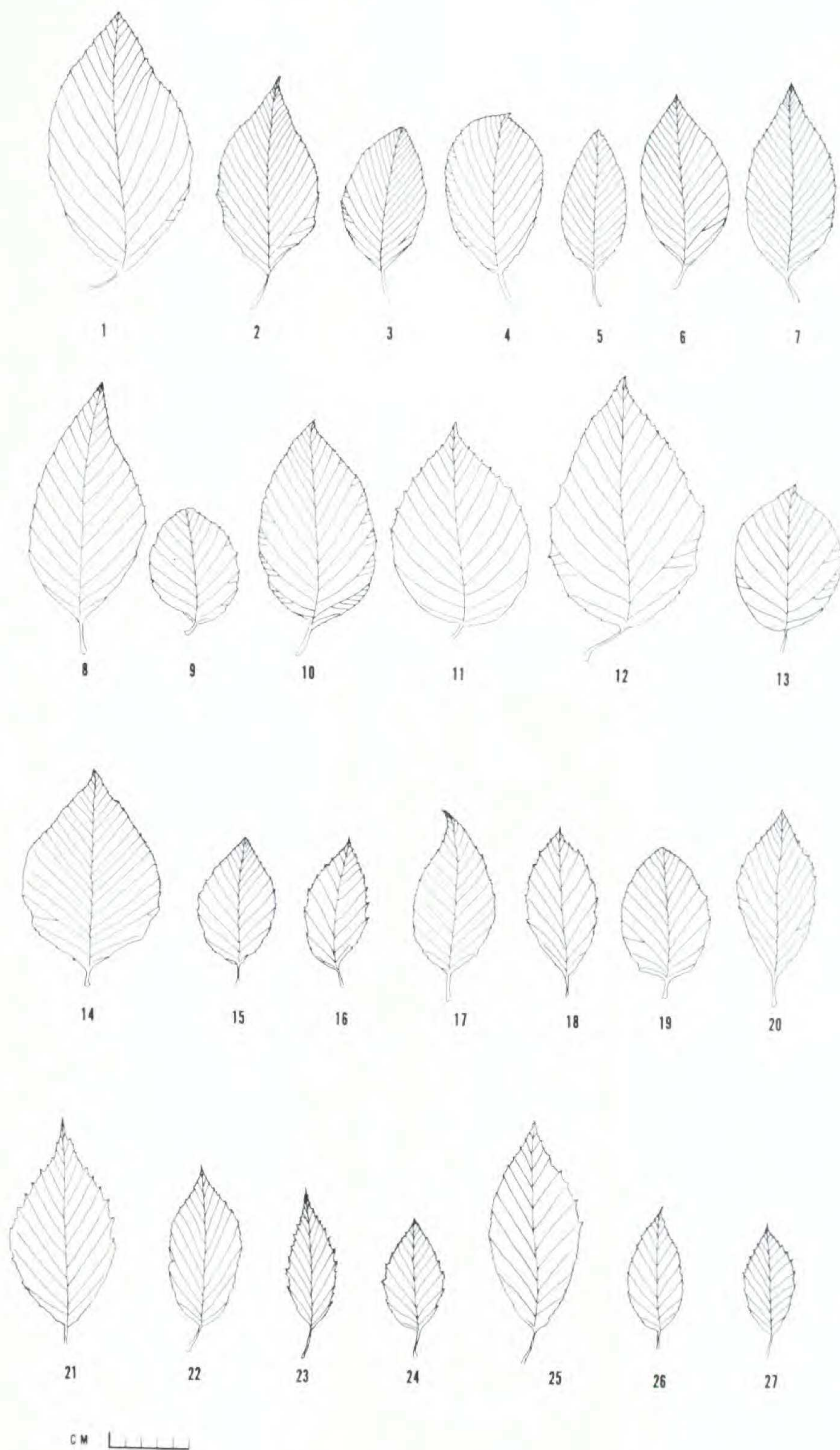


Figure 10. Outlines of leaves of *Alnus* showing extremes in the patterns of shape and margin variation: 1-10, *Alnus acuminata* ssp. *acuminata*; 11-20, *A. acuminata* ssp. *arguta*; 21-27, *A. acuminata* ssp. *glabrata*.

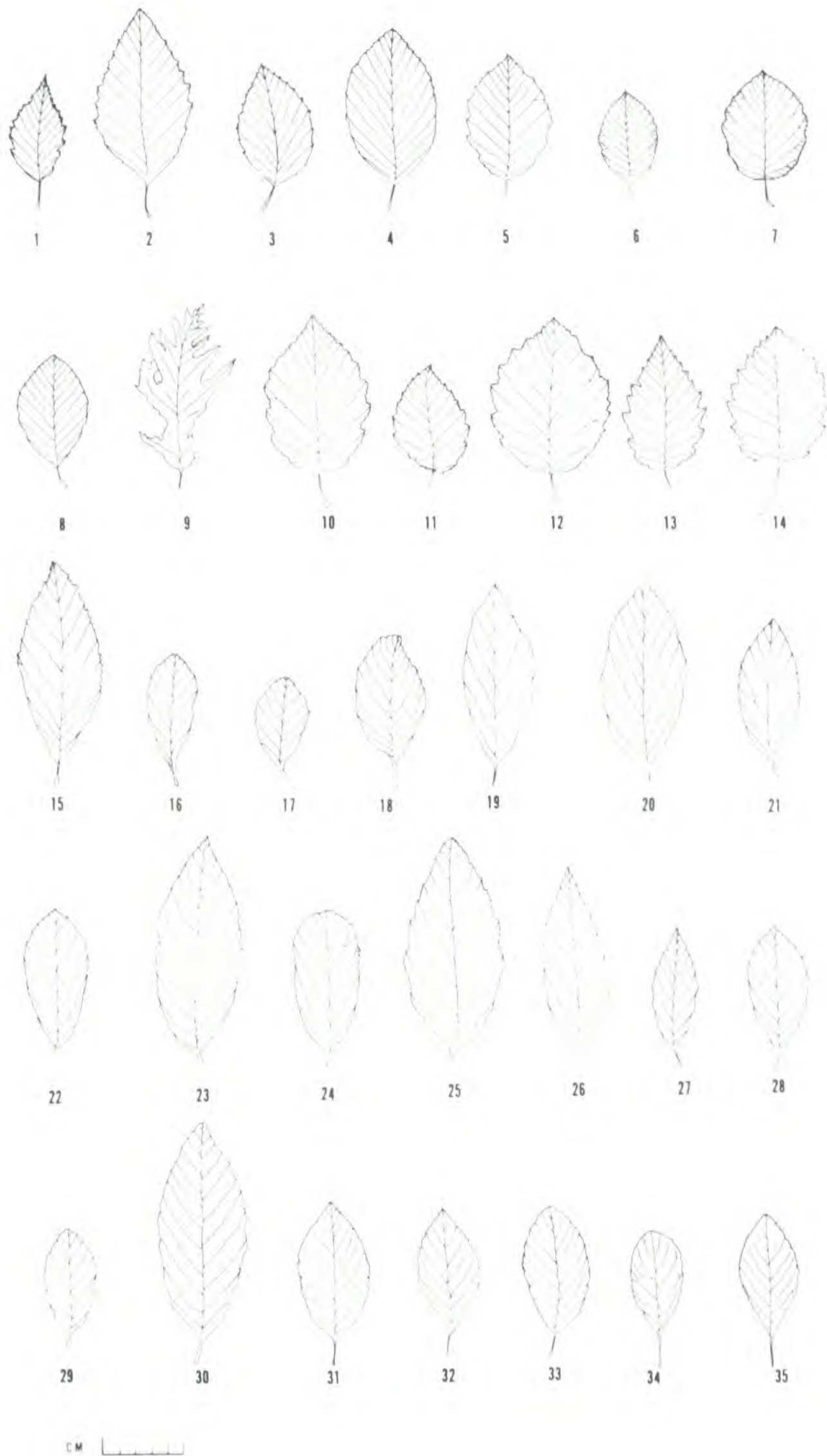


Figure 11. Outlines of leaves of *Alnus* showing extremes in the patterns of shape and margin variation: 1-4, *Alnus oblongifolia*; 5-9, *A. incana* ssp. *rugosa*; 10-14, *A. incana* ssp. *tenuifolia*; 15-21, *A. jorullensis* ssp. *jorullensis*; 22-30, *A. jorullensis* ssp. *lutea*; 31-35, *A. maritima*.

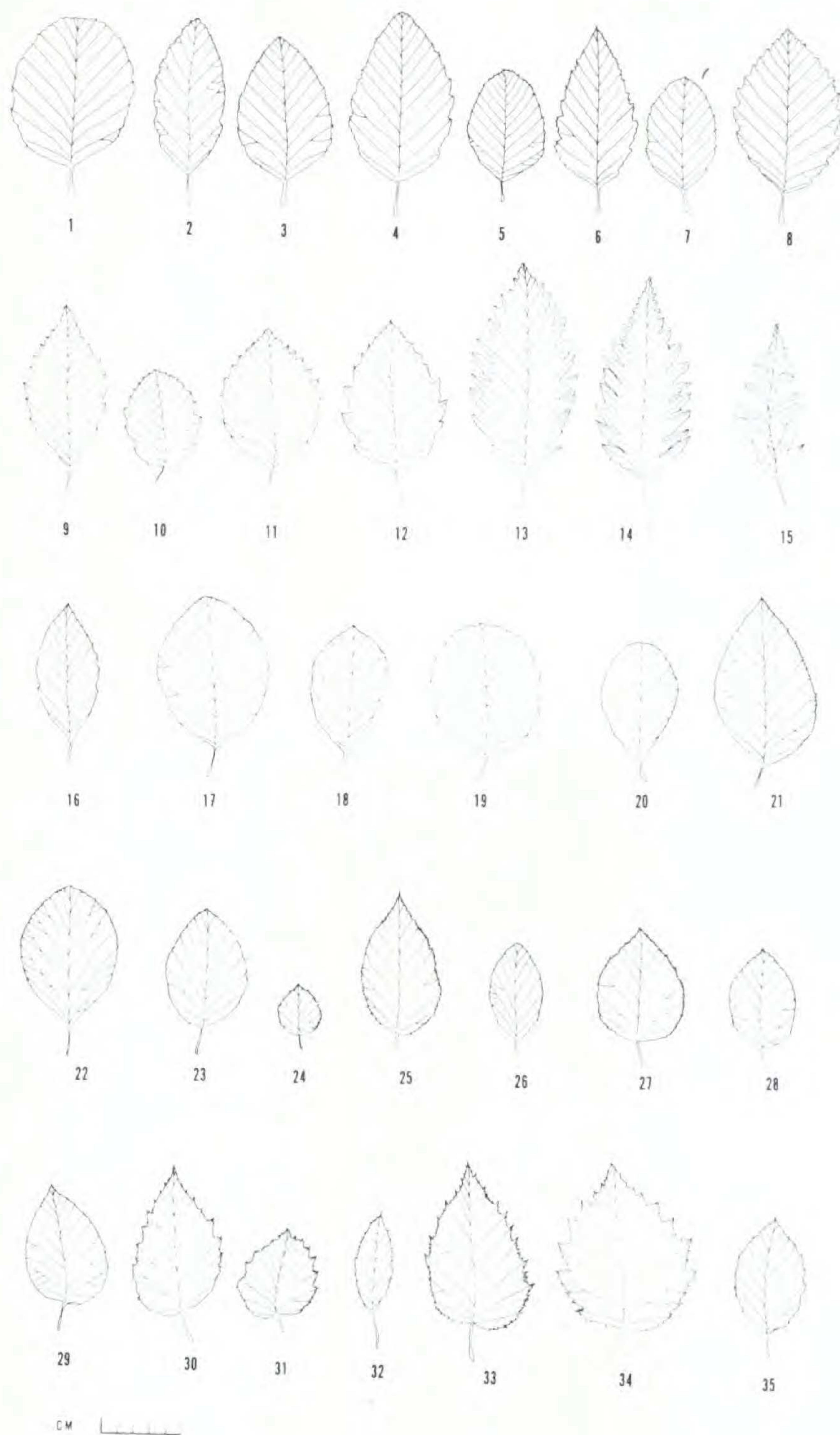


Figure 12. Outlines of leaves of *Alnus* showing extremes in the patterns of shape and margin variation: 1-7, *Alnus rhombifolia*; 8-15, *A. rubra*; 16-20, *A. serrulata*; 21-28, *A. viridis* ssp. *crispa*; 29-35, *A. viridis* ssp. *sinuata*.

catkins, which occasionally also appear in branched clusters on vigorous plants. In *A. viridis* and other members of subg. *Alnobetula*, the staminate and lower pistillate catkins retain the subtending leaves, which may be somewhat reduced in size, while in the other species, all or most of the leaves are lost and the internodes appreciably shortened. Sometimes pistillate catkins are seen on the staminate branches just below the staminate catkins, or staminate catkins may appear at the tips of the pistillate branches above the pistillate catkins. Occasionally, both pistillate and staminate flowers may appear in the same catkin and, in this case, the staminate are apical.

The pistillate catkins of *Alnus viridis* are pendent on long, thin peduncles. *Alnus maritima* has somewhat stouter and shorter peduncles, and the remainder of the species have still shorter ones, becoming nearly sessile in *A. incana* and *A. serrulata*. Where the pistillate catkins occur in racemose clusters, the catkins near the base of the cluster always have longer peduncles than those at the tip.

Murai (1964) regards the single, axillary pistillate catkins of *Alnus maritima* as advanced over the clustered type and shows a phylogenetic series of reduction leading to this state in the Asian members of subg. *Clethropsis*. In *Alnus maritima* nodes are evident on the "peduncle" of each solitary pistillate catkin, suggesting this reduction. That the short axillary pistillate branches in the subgenera *Alnus* and *Alnobetula* are already reduced from a primitive condition in which both pistillate and staminate catkins were present is suggested by the occasional presence of both kinds of inflorescences on the same branch. Similarly, that simple axillary staminate catkins are derived from branched systems is indicated by the occasional appearance of such systems in vigorous specimens.

At maturity, the pistillate catkins of all the alders become woody and cone-like, the five bracts of each cymule fusing into a single persistent scale bearing two fruits. These woody mature cones are often useful in identification, varying considerably in shape and size (Figures 16, 17, & 18). The cone scales also vary in shape and size, but this is mostly correlated with the dimensions of the cone itself. Other variation in the cone scales involves the shape, degree of thickening, and amount of reflexing of the terminal lobe. These woody infructescences are one of the most distinctive features of *Alnus* and the most useful in distinguishing it from the genus *Betula*.

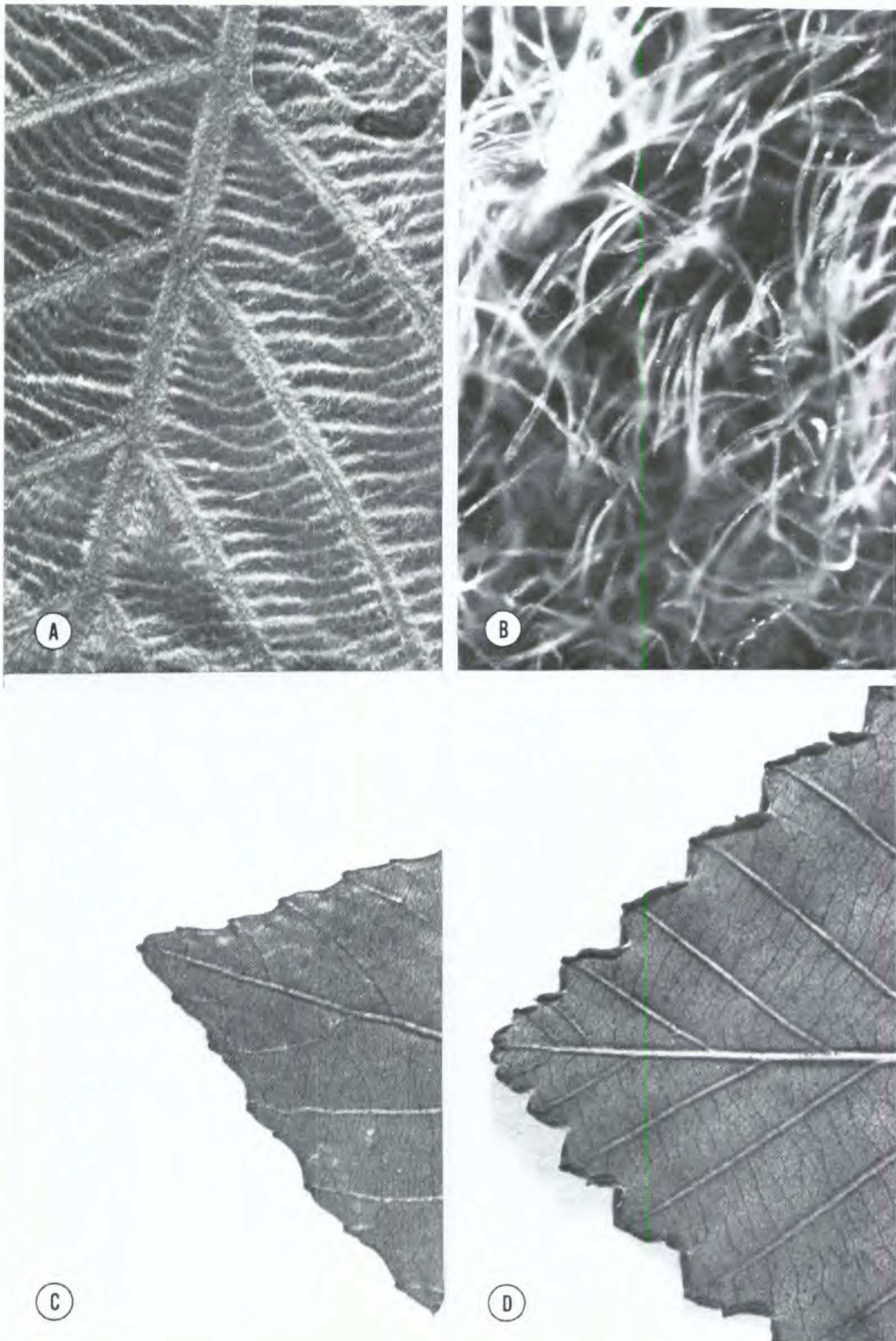


Figure 13. Macroscopic features of *Alnus* leaves. A, *Alnus viridis* ssp. *crispa*, pubescent extreme (*A. crispa* var. *mollis* Fern.), $\times 2$. B, same as A, $\times 30$. C, *A. maritima*, glandular teeth, $\times 2$. D, *A. rubra*, revolute margin, $\times 2$.

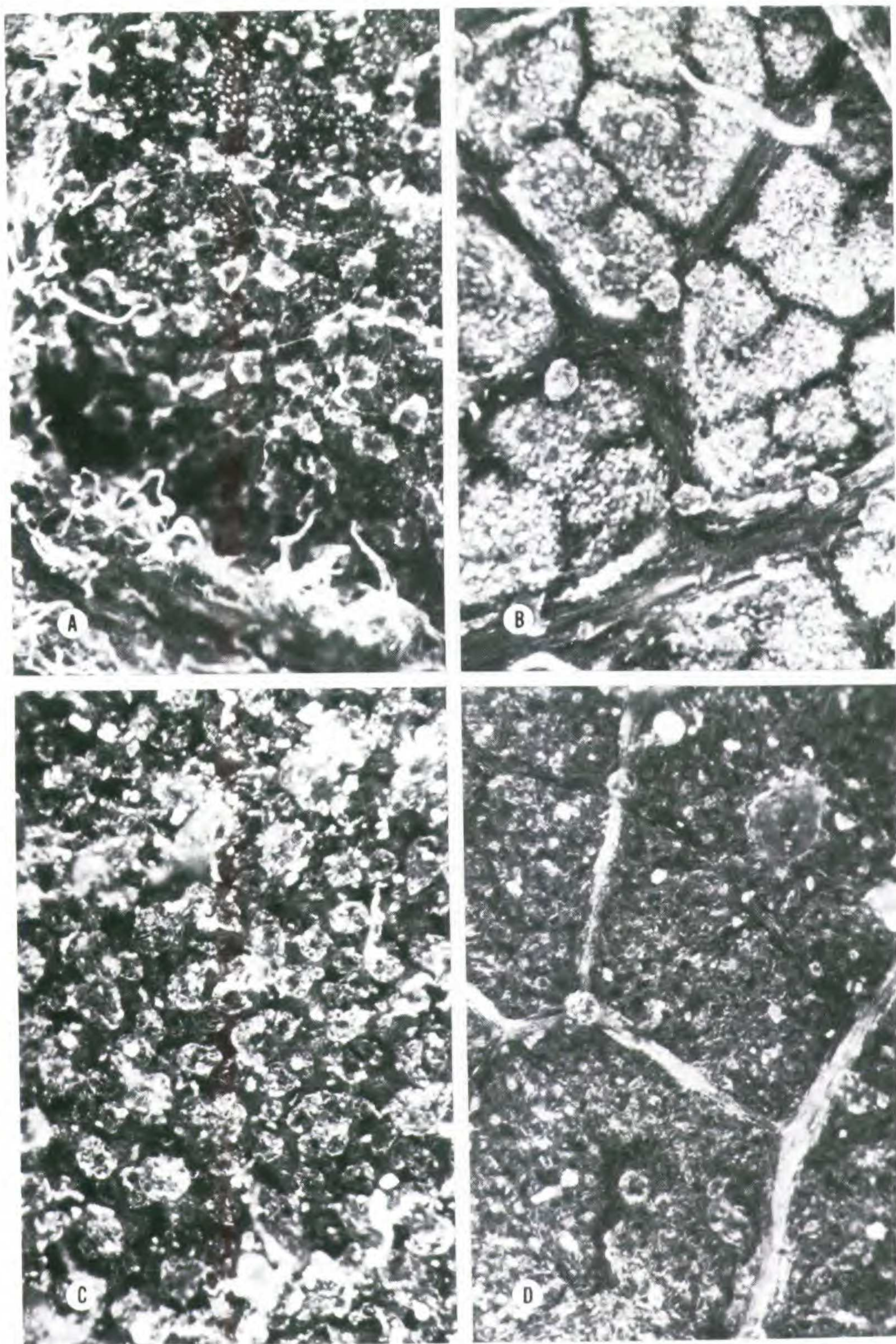


Figure 14. Epi-illuminated microscopic views of abaxial leaf surfaces of *Alnus* showing veins, resinous deposits, and glands, all $\times 30$. A, *Alnus acuminata* ssp. *arguta*. B, *A. jorullensis* ssp. *jorullensis*. C, *A. jorullensis* ssp. *lutea*. D, *A. viridis* ssp. *sinuata*.

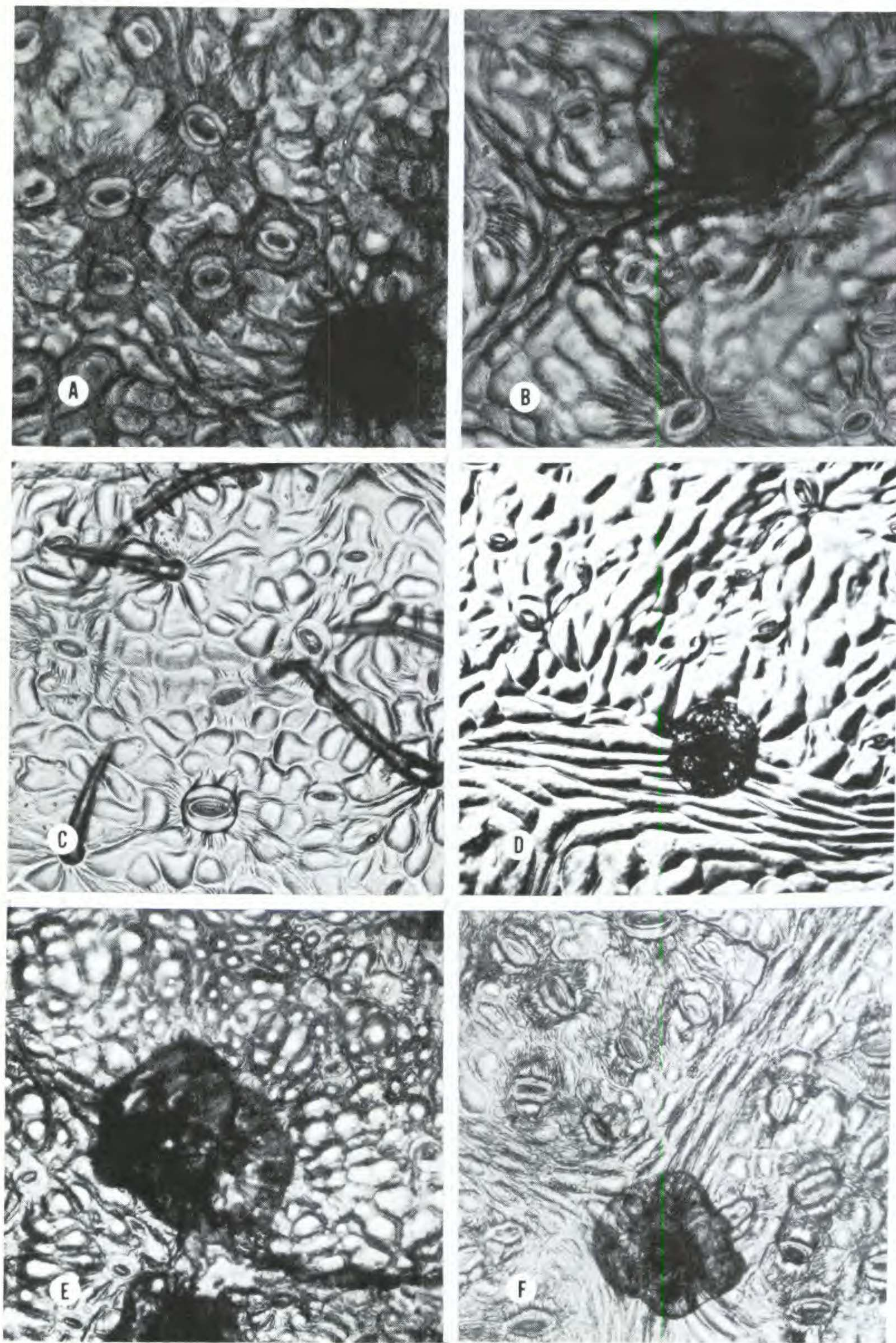


Figure 15. Photomicrographs of abaxial leaf cuticle imprints of *Alnus* made on thin acetate sheets showing stomata, epidermal cells, hairs, and glands, all $\times 105$. A, *Alnus acuminata* ssp. *arguta*. B, *A. acuminata* ssp. *glabrata*. C, *A. oblongifolia*. D, *A. incana* ssp. *tenuifolia*. E, *A. jorullensis* ssp. *lutea*. F, *A. maritima*.

Flowers. The flowers of *Alnus* are unisexual and minute, as in most other wind-pollinated plants. The staminate flowers have a tiny but well-formed perianth with from two to six parts, usually appearing to be a single whorl. Most species of *Alnus* and *Clethropsis* have four perianth parts and an equal number of stamens opposite them. *Alnus rhombifolia* commonly has only two perianth segments and two stamens, and *A. oblongifolia* usually has four, sometimes with two tepals and two stamens smaller than the other two. In *Alnus viridis*, four or five tepals and stamens are the rule, but occasionally up to six perianth parts and six stamens may be present, each in two whorls (Abbe, 1935).

The stamens vary in length and degree of fusion to the perianth parts. They are tetrasporangiate and never exerted very far from the catkin. In *Alnus incana*, the filaments are subsessile, never exceeding the length of the tepals. They are long in *A. viridis*, *A. maritima*, *A. oblongifolia*, *A. rhombifolia*, *A. rubra*, and *A. serrulata*, and intermediate in the remaining species. In *Alnus incana* of Europe, the filament length is variable.

The pistillate flowers are normally without a perianth, consisting mainly of a single bicarpellate ovary derived from a tricarpetate one, together with a simple two-branched style (Abbe, 1935; Hjelmqvist, 1948). Abbe (1938) noted that single tricarpetate pistils are often found in the axils of foliage leaves below the catkins. The ovary has two poorly-defined locules, becoming one above the single ovule in each section. The placentation is basically axile according to Abbe (1935); the ovules are anatropous, unitegmic, and crassinucellar (Davis, 1966).

The ovary in *Alnus* was shown to be inferior by Abbe (1935, 1938), who found that three or four small elongate glands of the type occurring on the edges of the perianth parts of the staminate flowers sometimes appear at the summit. In several specimens of *Alnus rubra* he found true tepals in this position, with the glands now at their apices. Four such glands were seen on the perianth parts of flowers from the Asian *A. subcordata*, while two appeared in specimens of *A. maritima*, *A. incana*, and *A. rubra* from North America. Vestigial vascular traces were seen running to the glands in the specimen of *A. incana*.

On the basis of staminate floral morphology, *Alnus viridis* is the most primitive species, having lost the fewest parts, and *A. oblongifolia* is the most advanced, having lost the most. Likewise, with

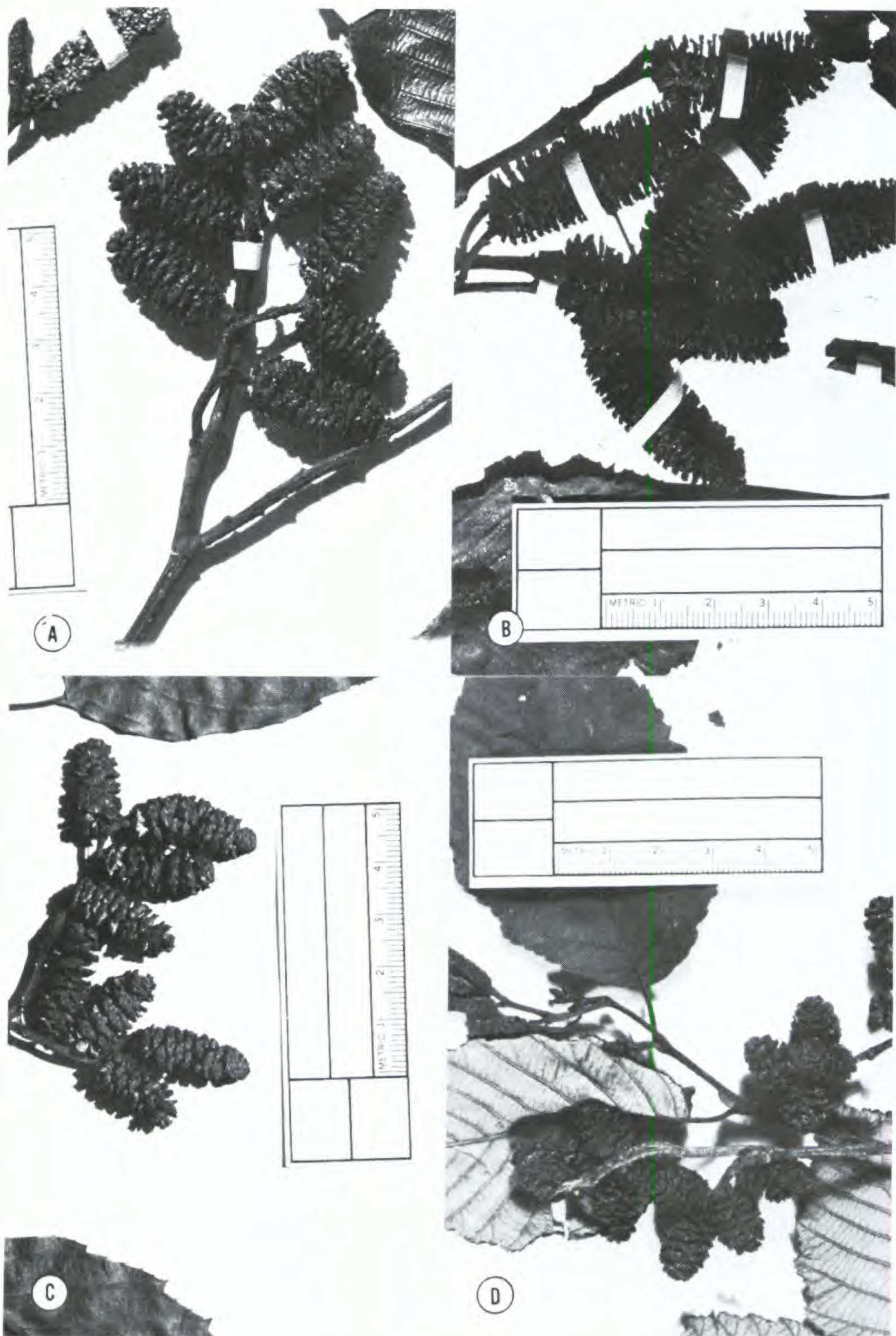


Figure 16. Mature infructescences of representative species of *Alnus*. A, *Alnus acuminata* ssp. *acuminata*. B, *A. acuminata* ssp. *arguta*. C, *A. acuminata* ssp. *glabrata*. D, *A. incana* ssp. *rugosa*.

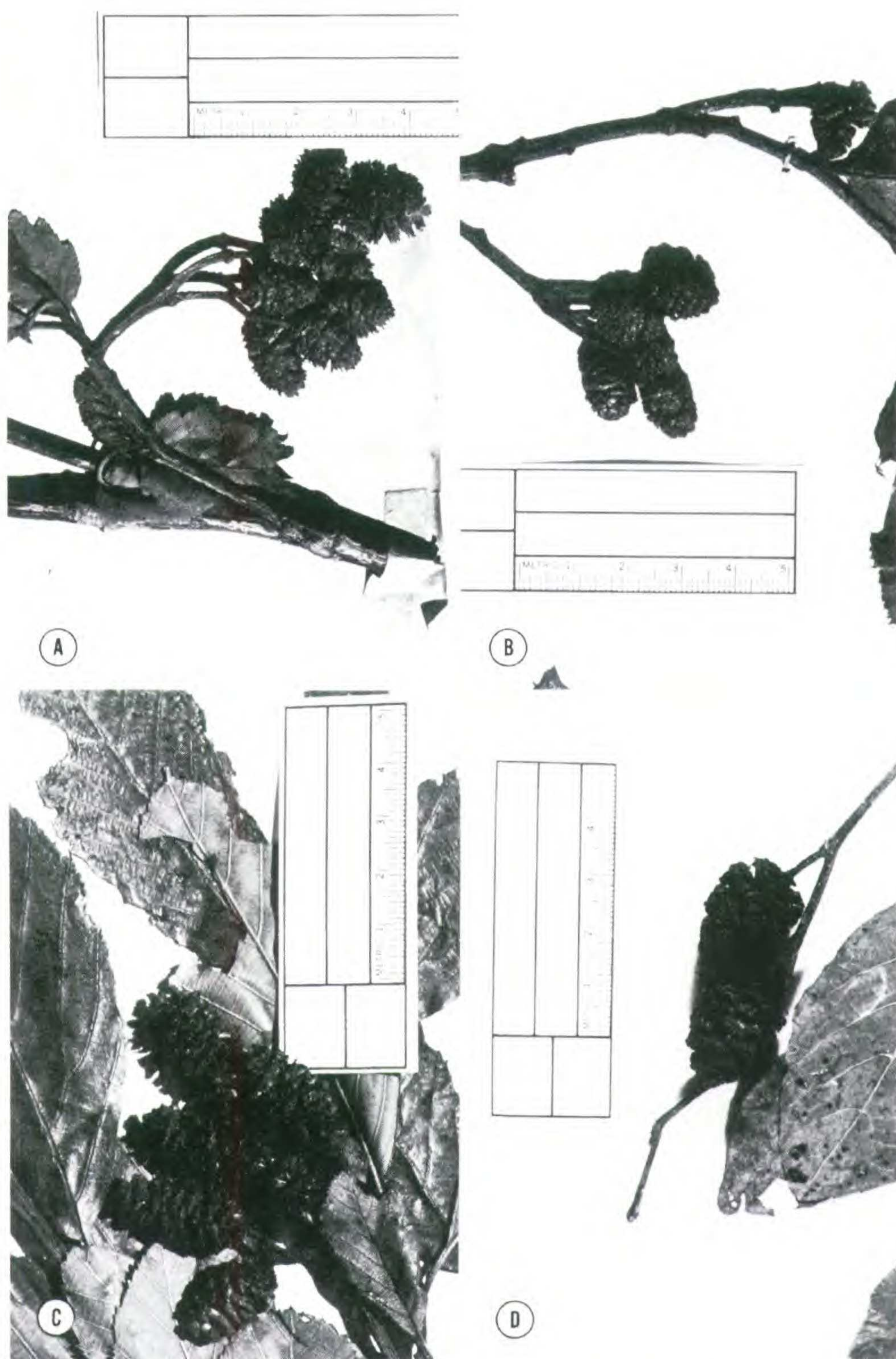


Figure 17. Mature infructescences of representative species of *Alnus*. A, *Alnus incana* ssp. *tenuifolia*. B, *A. jorullensis* ssp. *jorullensis*. C, *A. jorullensis* ssp. *lutea*. D, *A. maritima*.

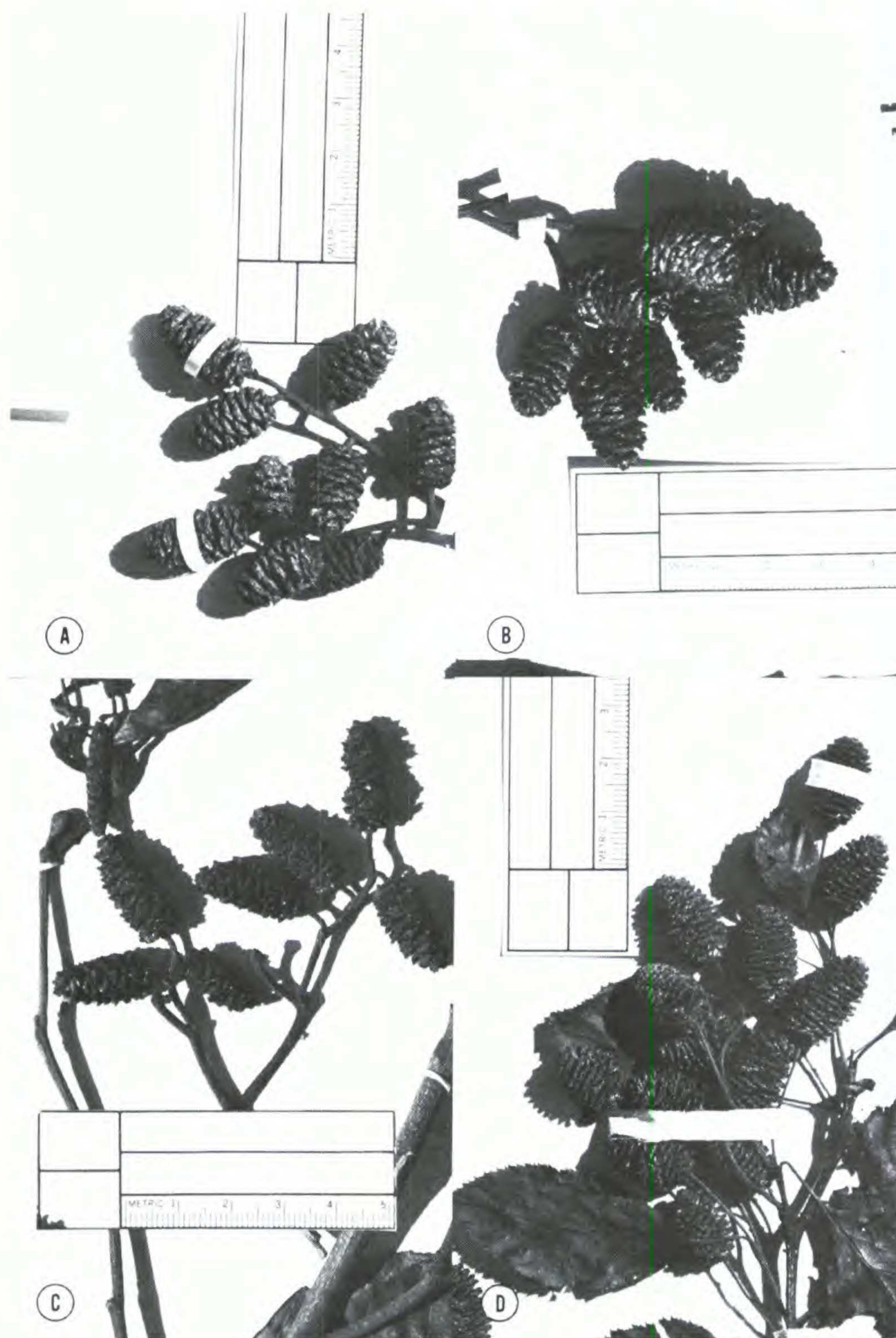


Figure 18. Mature infructescences of representative species of *Alnus*. A, *Alnus rhombifolia*. B, *A. rubra*. C, *A. serrulata*. D, *A. viridis* ssp. *sinuata*.

regard to inflorescences, *A. viridis* is the most primitive, but for this character *A. maritima* is the most advanced.

Pollen. Pollen grains of *Alnus* are small, light in weight, and produced in abundance. Erdtman (1969) estimates that a single catkin of *Alnus glutinosa* produces as many as 4,500,000 grains, compared with 1,250,000 in *Quercus robur* and 175,000 in *Fagus sylvatica*. The weight of a single grain is about 6.5×10^{-9} gm, compared with 3.8×10^{-9} gm in *Juniperus* and 37.0×10^{-9} gm in *Fagus* (Erdtman, 1969). Wodehouse (1935) states that alder pollen is "caught in great abundance on pollen slides exposed several miles from any trees." Where *Alnus* is abundant, the windborn pollen is sometimes responsible for causing hayfever in susceptible individuals (Chamberlain, 1927).

The grains are isopolar, radiosymmetric, stephanoporate monads ranging from 17 to 35 microns in diameter. They are somewhat flattened, and they typically have from three to six apertures, though occasionally more than six pores may be present. The apertures are aspidate and often somewhat elliptical, ranging from 2.5 to 4.5 microns long. Each aperture has an annulus. The surface is smooth or slightly granular in appearance under the compound microscope (Figure 19) but can be seen to be covered with very minute verrucae, gemmae, or spinules (nanoverrucae, nanogemmae, or nanospinules) positioned on low ridges when viewed with the scanning electron microscope (Figure 20). The sexine is pertectate and thicker than the nexine (Erdtman, 1969). Thickened bands (arcus) in the exine (tectum and nexine) run in pairs from aperture to aperture, giving a very characteristic appearance to shrunken or collapsed grains (Figure 20), although these bands are not always evident in fully expanded and unstained material. Below the pores, the intine is thickened considerably to form large onci.

To find morphological differences in the pollen of *Alnus* species, grains were examined using both light and scanning electron microscopy, as discussed by Ridgway and Skvarla (1969). Pollen from three to seven herbarium specimens of each species was collected and mounted in glycerine jelly prepared by the formula of Johanssen (1940) and stained light red with safranin-O. Within one week after preparation these grains were studied, measured, and photographed under oil immersion at a magnification of $630\times$ with a Zeiss Photomicroscope II. Seven grains on each slide (21 to 49

Table 1. Herbarium specimens from which pollen was obtained for study.

Alnus acuminata ssp. *acuminata*:

- Balls 6924, Peru (F)
 Killip & Smith 17928, Dept. Santander, Colombia (NY)
 Tovar 2770, Prov. Huancayo, Peru (UC)
 Venturi 1047, Prov. Tucumán, Argentina (F)
 Venturi 3865, Prov. Tucumán, Argentina (MO)

Alnus acuminata ssp. *arguta*:

- Breedlove 7851, Chenalho, Chiapas, México (F)
 Breedlove 8572, San Juan Ixcay, Guatemala (F)
 Breedlove 9063, Tenejapa, Chiapas, México (MICH)
 Carlson 2412, Las Casas, Chiapas, México (MICH)
 Espinosa 641, Cañada de Contreras, D. F., México (ENCB)
 Hinton 15415, Distr. Mina, Guerrero, México (MICH)
 Lems 5031, Prov. Cartago, Costa Rica (NY)
 Palacios s.n., Jan. 19, 1968, Zacapoaxtla, Puebla (ENCB)
 Standley 80553, Volcán de Pacaya, Guatemala (F)
 Steyermark 34605, Volcán Zunil, Guatemala (F)

Alnus acuminata ssp. *glabrata*:

- Mexia 8979, Petlacala, Guerrero, México (NY)
 Pringle 8022, Tizapán, D. F., México (MEXU)
 Rzedowski 19301, Los Remedios, México, México (MSC)
 Rzedowski 26680, Distr. Coixtlahuaca, Oaxaca, México (ENCB)
 Torres 345, D. F., México (MEXU)

Alnus incana ssp. *incana*:

- Jaques s.n., Switzerland (RM)
 Markland s.n., Finland (DAO)
 Rozsebersky s.n., Hungary (UC)
 Tullberg s.n., Sweden (NY)

Alnus incana ssp. *rugosa*:

- Blanchard s.n., Caledonia Co., Vermont (GH)
 Dodge s.n., St. Clair Co., Michigan (RM)
 Fernald & Bartlett 10, Essex Co., Massachusetts (GH)
 Gilbert s.n., Berkshire Co., Massachusetts (UC)
 Lakela 1341, Louis Co., Minnesota (NY)
 Lucy 3238, Chenago Co., New York (F)
 Minshall 2707, Carleton Co., Ontario (DAO)
 Pepoon 630, Cass Co., Michigan (MSC)
 Ricard & Boivin 600, Quebec (UC)

Alnus incana ssp. *tenuifolia*:

- Breitung s.n., Alberta (DAO)
 Frost s.n., Colorado (UC)
 Keck 5526, Douglas Co., Nevada (UC)

Table 1 (continued)

Robbins 1699, El Dorado Co., California (UC)

Russell 4862, Sutherland, Saskatchewan (DAO)

Turner 4784, Alberta (DAO)

Alnus jorullensis ssp. *jorullensis*:

Rzedowski 2239, San Angel, D. F., México (ENCB)

Rzedowski 22045, Cerro Ajusco, D. F., México (ENCB)

Rzedowski 27147, El Guajolote, Hidalgo, México (ENCB)

Alnus jorullensis ssp. *lutea*:

Breedlove 16518, Sierra Surutato, Sinaloa, México (MICH)

Rzedowski 19395, Nevado de Colima, Jalisco, México (ENCB)

Salazar 5, San Angel, D. F., México (MEXU)

Alnus maritima

Commons s.n., Wicomico Co., Maryland (NY)

Furlow 205, Sussex Co., Delaware (MSC)

Robbins 2795, Pontotoc Co., Oklahoma (DAO)

Smith s.n., Sussex Co., Delaware (RM)

Waterfall 9258, Johnston Co., Oklahoma (OKLA)

Alnus oblongifolia:

Foster & Arnold 108, Gila Co., Arizona (US)

Furlow s.n., Graham Co., Arizona (MSC)

Greene s.n., Grant Co., New Mexico (MO)

Hartman 322, Huchuerachi, Sonora, México (F)

Toumey s.n., Pima Co., Arizona (RM)

Alnus rhombifolia:

Applegate 960, Jackson Co., Oregon (UC)

Heller 11167, Butte Co., California (NY)

Parks & Parks 24084, Del Norte Co., California (RM)

Plaskett 14, Monterey Co., California (RM)

Suksdorf s.n., Klickitat Co., Washington (F)

Tracy 5306, Humboldt Co., California (UC)

Wapole 150, Jackson Co., Oregon (US)

Alnus rubra:

Henderson 312, Hood River Co., Oregon (NY)

Lawfer 131, Marin Co., California (WTU)

Macoun s.n., Victoria, British Columbia (CAN)

Sheldon S.11680, Clarke Co., Washington (UC)

Tracy 6151, Humboldt Co., California (UC)

Alnus serrulata:

Demaree 16650, Hot Springs Co., Arkansas (NY)

Furlow 344, Brown Co., Indiana (MSC)

Table 1 (continued)

Godfrey 55316, Jefferson Co., Florida (NY)

Johnson 2619, Easton Co., Connecticut (F)

Alnus viridis ssp. *crispa*:

Baldwin et al. 559, Baie James Co., Quebec (CAN)

Churchill s.n., July 10, 1937, Coos Co., New Hampshire (MSC)

Cody & Webster 5362, Alaska (DAO)

Dumais & Rankin 1002, Alberta (CAN)

Forbes s.n., May 11, 1912, Franklin Co., Massachusetts (UC)

Furlow 251, Mitchell Co., North Carolina (MSC)

Young s.n., May 21, 1940, Kenora Distr., Ontario (DAO)

Alnus viridis ssp. *sinuata*:

Anderson 6479, Alaska (RM)

Bacigalupi et al. 3469, Josephine Co., Oregon (UC)

Furlow 279, Lemhi Co., Idaho (MSC)

Sanson 1630, Alberta (DAO)

Schmantz 367, Missoula Co., Montana (DAO)

Alnus viridis ssp. *viridis*:

Bornmüller s.n., Oct., 1919, Germany (A)

Kampstein s.n., without date, Austria (US)

Prerowsky s.n., Apr., 1893, Bohemia (DAO)

Vautier et al. s.n., May 28, 1963, France (WTU)

grains per species) were measured to determine diameters, and 100 grains per slide (300 to 900 grains per species) were examined to establish the average number of pores per grain. For scanning electron microscopy, pollen collected from herbarium specimens was attached to metal stubs by means of double-adhesive cellophane tape, coated with gold, and examined with an Advanced Metals Research Model 900 scanning electron microscope at Michigan State University. Herbarium specimens used for the collection of pollen grains are listed in Table 1.

Few tangible differences, other than pore number and grain diameter, were noted in the material studied, although slight variations in the color of the grains, the sculpturing of the surface, and the size of the aspides and onci were detectable. The size ranges of the grains of all species overlap (Table 2, Figure 21), but the mean values of some, such as *Alnus maritima*, which has very small grains, are useful in distinguishing them from the other taxa. The least significant difference among the mean values (L.S.D. Test) was

found to be 0.836 microns at the 5% probability level and 1.099 microns at the 1% level. Based on pollen diameter, three major groups can be recognized readily, these corresponding roughly to the three subgenera. *Alnus maritima* (subg. *Clethropsis*) has the smallest grains, showing an average diameter of only 19.7 microns. Subgenus *Alnobetula*, represented by *A. viridis*, has larger grains, with mean diameters ranging from 21.1 to 22.1 microns, and the remaining species, members of subg. *Alnus*, have still larger mean diameters, ranging from 21.1 to 25.0 microns.

Aperture number is often a better criterion for distinguishing species than is grain diameter, as shown in Table 2. *Alnus maritima* and *A. serrulata* typically have grains with four pores, while five taxa (*A. viridis* ssp. *crispa*, *A. viridis* ssp. *sinuata*, *A. viridis* ssp. *viridis*, *A. jorullensis*, and *A. rubra*) usually demonstrate a five-pored configuration. Two taxa (*A. incana* ssp. *rugosa* and *incana*) have either four- or five-pored grains, these occurring in about a one to one ratio, and six taxa (*A. oblongifolia*, *A. rhombifolia*, *A. incana* ssp. *tenuifolia*, *A. acuminata* ssp. *acuminata*, *A. acuminata* ssp. *arguta*, and *A. acuminata* ssp. *glabrata*) have both four- and five-pored grains in ratios of two or three to one. In most cases, variability in pore number is high, with up to 35% of the grains of a particular specimen lying outside the "typical" number.

Alnus incana ssp. *tenuifolia* demonstrates a tendency toward the four-pored condition shown by *A. serrulata*. The four-pored condition might be considered advanced in *Alnus*, even though a small number of apertures is probably the ultimate primitive condition, as suggested by Doyle (1969). That four pores is an advanced condition in *Alnus* is indicated by the fact that it occurs mainly in species that are otherwise quite specialized (*A. serrulata* and *A. maritima*) while those taxa having five or six pores (*A. viridis* subspecies) are otherwise more generalized. In addition, the fact that "in fossil alder pollen from the Tertiary of west Scotland, increased aperture number is linked with a tendency towards a panotreme condition" (Erdtman, 1969) could be interpreted to support this idea.

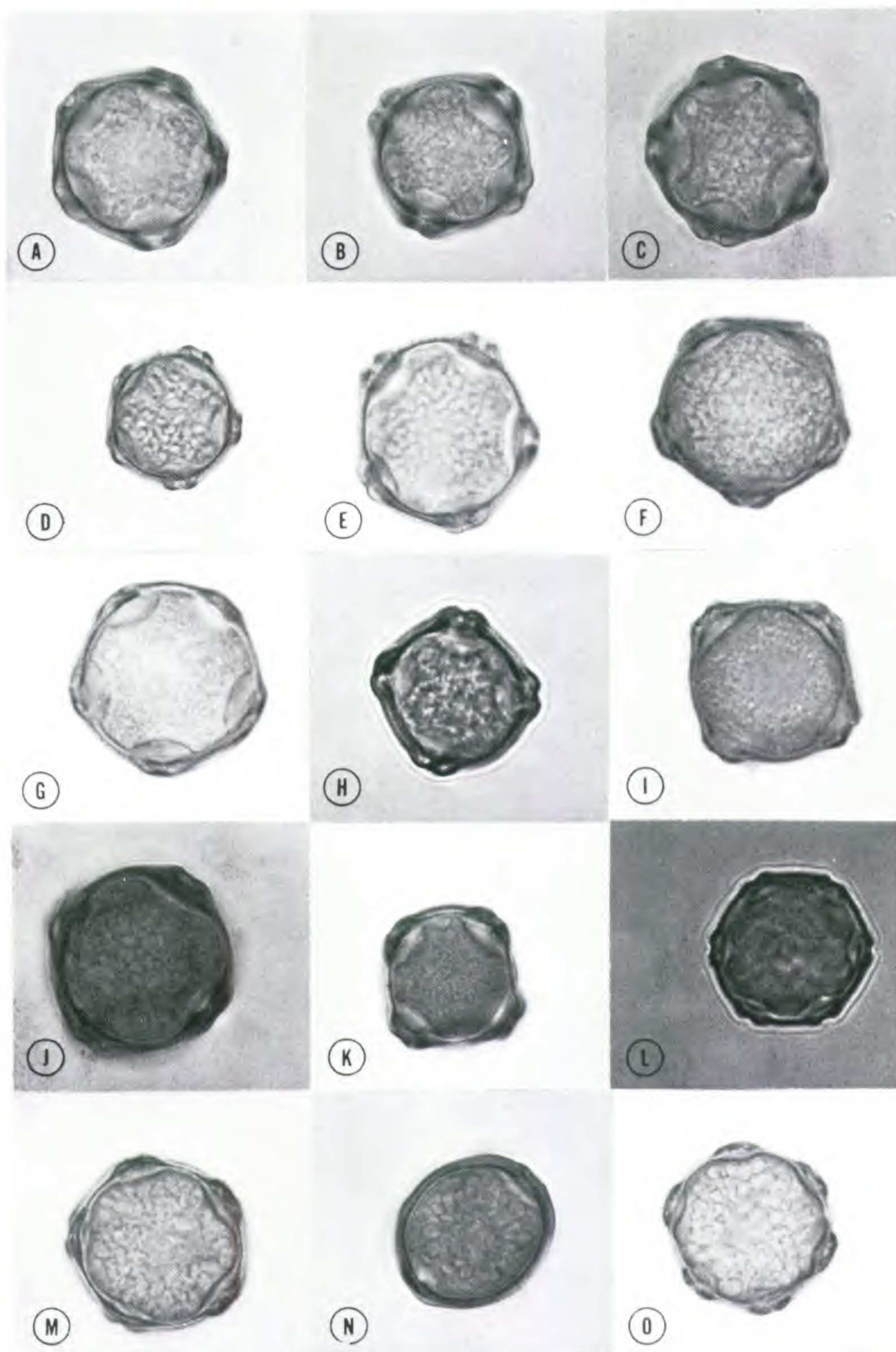
Four groups of species can be distinguished on the basis of surface sculpturing, as seen in scanning electron micrographs (Figure 20). The first of these, represented by *Alnus viridis* spp. *crispa* and *sinuata*, shows grain surfaces densely covered with prominent gemmae positioned along short low ridges, the elements being larger in ssp. *sinuata*. A second group, represented by *A.*

Table 2. Size of *Alnus* pollen grains (microns)

Taxon	Mean Diameter	Range	Standard Deviation
<i>A. acuminata</i> ssp. <i>acuminata</i>	24.22	20.9–28.7	1.80
<i>A. acuminata</i> ssp. <i>arguta</i>	20.80	18.6–27.1	1.61
<i>A. acuminata</i> ssp. <i>glabrata</i>	23.78	20.2–26.4	1.52
<i>A. incana</i> ssp. <i>incana</i>	24.49	18.6–29.5	3.10
<i>A. incana</i> ssp. <i>rugosa</i>	22.80	19.4–25.6	1.62
<i>A. incana</i> ssp. <i>tenuifolia</i>	23.60	18.6–27.9	2.00
<i>A. jorullensis</i> ssp. <i>jorullensis</i>	23.14	20.2–26.4	2.11
<i>A. jorullensis</i> ssp. <i>lutea</i>	24.34	21.7–27.9	1.60
<i>A. maritima</i>	19.67	17.1–23.3	1.72
<i>A. oblongifolia</i>	24.34	20.2–27.9	1.94
<i>A. rhombifolia</i>	24.51	21.7–28.7	1.52
<i>A. rubra</i>	25.02	20.0–27.9	1.99
<i>A. serrulata</i>	21.06	18.6–24.8	1.90
<i>A. viridis</i> ssp. <i>crispa</i>	21.06	18.6–23.3	1.46
<i>A. viridis</i> ssp. <i>sinuata</i>	21.83	17.1–26.4	2.01
<i>A. viridis</i> ssp. <i>viridis</i>	22.08	18.6–26.4	1.84

Table 3. Percent of *Alnus* pollen grains having various numbers of pores.

Species	Number of Pores			
	3	4	5	6
<i>A. acuminata</i> ssp. <i>acuminata</i>	0.0	23.8	73.0	3.2
<i>A. acuminata</i> ssp. <i>arguta</i>	0.0	34.6	65.4	0.0
<i>A. acuminata</i> ssp. <i>glabrata</i>	0.0	31.6	67.8	0.6
<i>A. incana</i> ssp. <i>incana</i>	0.0	38.0	58.6	3.4
<i>A. incana</i> ssp. <i>rugosa</i>	0.0	46.8	51.4	1.8
<i>A. incana</i> ssp. <i>tenuifolia</i>	0.0	70.3	29.8	0.0
<i>A. jorullensis</i> ssp. <i>jorullensis</i>	0.0	14.3	82.0	3.7
<i>A. jorullensis</i> ssp. <i>lutea</i>	0.0	14.4	82.0	3.4
<i>A. maritima</i>	6.0	86.0	8.0	0.0
<i>A. oblongifolia</i>	0.0	33.2	64.6	2.2
<i>A. rhombifolia</i> —	0.0	23.4	76.0	0.6
<i>A. rubra</i>	0.0	7.8	76.0	16.2
<i>A. serrulata</i>	11.0	80.6	8.4	0.0
<i>A. viridis</i> ssp. <i>crispa</i>	0.4	10.2	82.0	7.4
<i>A. viridis</i> ssp. <i>sinuata</i>	0.0	9.6	82.4	0.0
<i>A. viridis</i> ssp. <i>viridis</i>	0.0	7.4	77.2	15.4



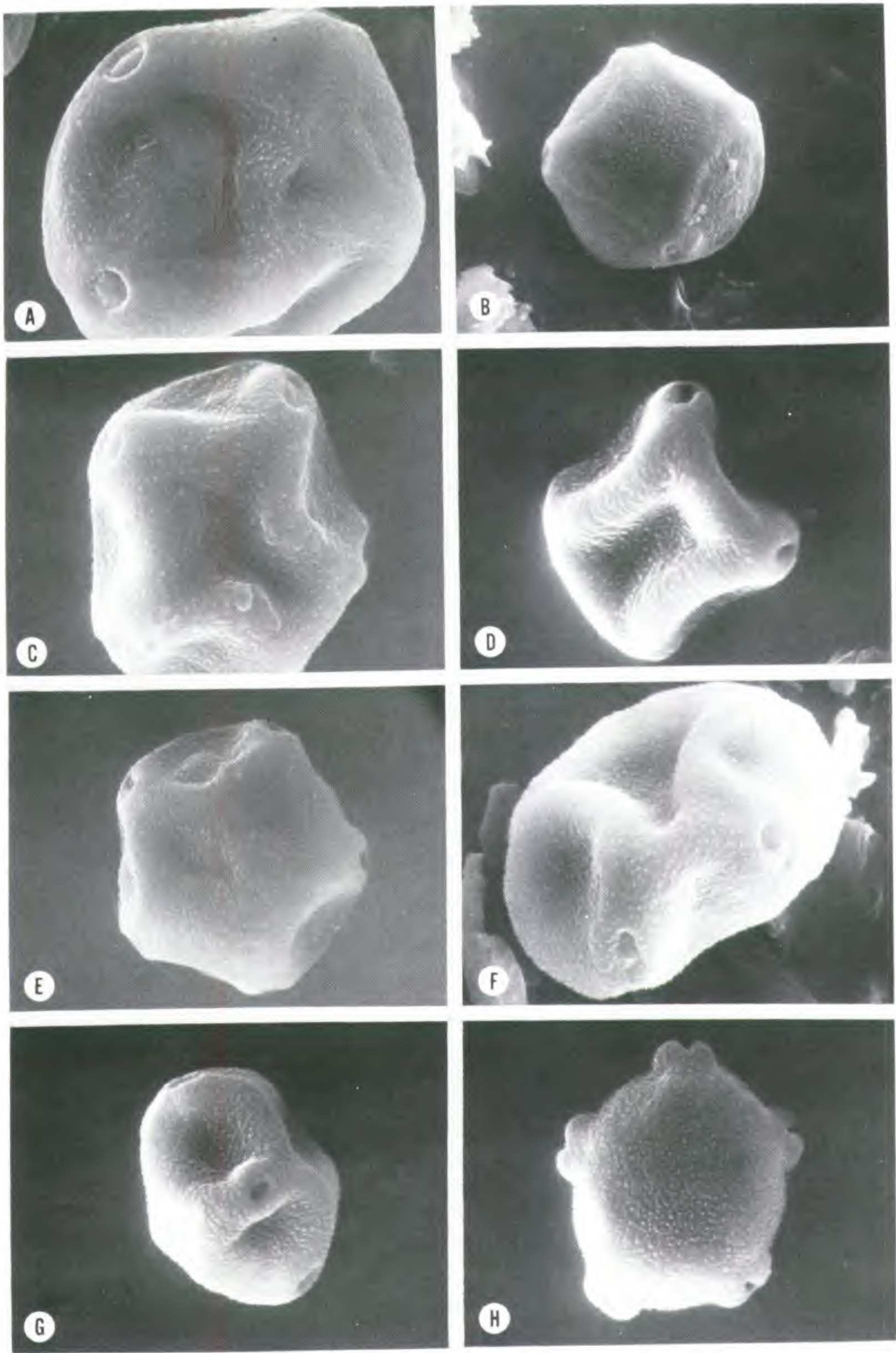
serrulata, *A. incana* ssp. *rugosa*, and *A. incana* ssp. *tenuifolia*, has fairly dense verrucae, these positioned along longer and more prominent ridges. The verrucae are very dense in *A. incana* ssp. *tenuifolia* and *A. serrulata* and somewhat less so in *A. incana* ssp. *rugosa*. A third group, containing *A. acuminata* ssp. *acuminata*, *A. acuminata* ssp. *glabrata*, *A. jorullensis*, *A. rubra*, and *A. rhombifolia*, has low, moderately long ridges with only moderately dense verrucae. Finally, *A. maritima* shows pronounced long ridges with very small and infrequent elements.

With the light microscope, pollen from subg. *Alnobetula* may be distinguished from that of species in the other subgenera in that it is generally lighter in color (not as deeply stained by safranin) and has smaller onci and aspides, which give the grains a rounder or less angular appearance. *Alnus acuminata* has rather light-appearing grains, but not as light as those of subg. *Alnobetula*, and they bear medium to large aspides and onci. *Alnus incana* spp. *rugosa* and *tenuifolia*, as well as *A. serrulata*, *A. oblongifolia*, and *A. rhombifolia* all have medium to large aspides and onci and dark walls, while *A. maritima* and *A. rubra* have grains of similar shape but of intermediate shade. Finally, *A. jorullensis* bears relatively small aspides, medium-sized onci, and is of intermediate darkness.

Major groups of species based on pollen characteristics correlate well with clusters formed using gross plant structure. The subspecies of *Alnus viridis* form one group, *A. incana* and *A. serrulata* another, and *A. acuminata* a third. *Alnus jorullensis*, while clearly related to the *A. acuminata* complex, retains an identity of its own. *Alnus rubra*, *A. rhombifolia*, and *A. oblongifolia* appear to be most closely allied to the *A. acuminata* group.

Fruits. The fruits of *Alnus* are small, smooth-surfaced, light, dry, indehiscent, and laterally-winged (Figure 22). In the literature they have been termed both nutlets and samaras. In *Alnus viridis*, each wing is as wide as or wider than the body of the fruit itself, while

Figure 19. Pollen grains of representative species of *Alnus*, all $\times 865$. A, *Alnus acuminata* ssp. *arguta*. B, *A. oblongifolia*. C, *A. acuminata* ssp. *glabrata*. D, *A. incana* ssp. *incana*. E, *A. incana* ssp. *tenuifolia*. F, *A. jorullensis* ssp. *jorullensis*. G, *A. jorullensis* ssp. *lutea*. H, *A. maritima*. I, *A. rhombifolia*. J, *A. rubra*. K, *A. serrulata*. L, *A. viridis* ssp. *crispa*. M & N, *A. viridis* ssp. *sinuata*. O, *A. viridis* ssp. *viridis*.



other species have narrower wings. A few taxa (e.g., *A. maritima*) are characterized by essentially wingless fruits, there being only low ridges where the wings would otherwise occur. In these species dispersal is apparently by water, although even without wings the fruits may be carried some distance by moderately strong winds. The summit of the fruit is crowned by two persistent styles. The fruit body is usually elliptical in shape, and the wings, when present, are normally wider at the summit than below and extend further, both at the apex and base, than the body.

REPRODUCTIVE BIOLOGY

The alders are anemophilous, although insects are sometimes attracted to the staminate catkins (Figure 23). Species of subgenera *Alnus* and *Alnobetula* flower early in the spring in the temperate zone, from November to February in southern Mexico and Central America, and as late as July in northern Canada, while those of subg. *Clethropsis* bloom in the early autumn (September or October in *Alnus maritima*). In subg. *Alnus*, both staminate and pistillate catkins are produced during the growing season prior to blooming and are exposed during the winter. In subg. *Alnobetula*, only the staminate catkins are produced during the prior growing season and exposed during the winter, the pistillate catkins appearing along with the new foliage. Members of subg. *Clethropsis* produce both staminate and pistillate catkins during the same season as flowering. Anthesis takes place before the leaves appear in subg. *Alnus*, while the leaves are still small or just emerging from the bud in subg. *Alnobetula*, and when the plants are fully leafed out in subg. *Clethropsis*.

Staminate meiosis was found by Wetzel (1929) to occur in late summer (September) in members of subg. *Alnus* (*A. rubra*, *A. glutinosa*, and *A. cordata*) and somewhat earlier (July and August) in subg. *Alnobetula* (*A. viridis*). Meiosis occurs in August and September (immediately before anthesis) in subg. *Clethropsis* (*A. maritima*).

Figure 20. Scanning electron micrographs of pollen grains of representative species of *Alnus*. A, *Alnus incana* ssp. *rugosa*, $\times 1667$. B, *A. incana* ssp. *tenuifolia*, $\times 1000$. C, *A. jorullensis* ssp. *lutea*, $\times 1500$. D, *A. maritima*, $\times 1500$. E, *A. rubra*, $\times 1500$. F, *A. viridis* ssp. *crispa*, $\times 1500$. G, *A. viridis* ssp. *sinuata*, $\times 1500$. H, *A. viridis* ssp. *sinuata*, $\times 1500$.

McVean (1953a) reports that *Alnus glutinosa* is nearly always protogynous, although up to 12 percent protandry has been observed. Casual observation of the American species indicates that this general pattern may be true for them as well, although no definite data are available.

The age of first flowering of most species of *Alnus* is not known, but it probably occurs early in the life of at least the shrubby species. Lawrence (1958) reports that *A. viridis* ssp. *sinuata* in Alaska reaches flowering age in less than seven years. A specimen of *A. maritima* grown in an experimental garden in East Lansing, Michigan reached reproductive maturity at the age of three years, as determined from annual rings. Individuals of *A. viridis* ssp. *crispa*, *A. incana* ssp. *rugosa*, and *A. serrulata* grown in the same garden all reproduced first at the age of five years. The tree-sized species (*A. rubra*, *A. rhombifolia*, *A. acuminata*, *A. jorullensis*, etc.) were in general not seen reproducing in the field until they were relatively large.

To plants living in an environment with a relatively short growing season and a severe winter (such as that of far northern and subalpine climates) the parallel development of the shrub habit and an earlier reproductive maturity would be advantageous. Structural reduction under such environmental conditions seems to be associated with anatomical immaturity in otherwise adult plants (i.e., neoteny), as noted by Forsaith (1920) and Hall (1952).

Alnus frequently occurs in thickets, but it is not known whether such groups of plants always (or ever) represent clones. In the field, small plants of *A. serrulata*, *A. incana* ssp. *rugosa* and *tenuifolia*, *A. viridis* ssp. *sinuata*, and *A. oblongifolia* were occasionally found to be interconnected by their roots when dug for transplanting. Sprouting from exposed roots in streams was noted in *Alnus incana* ssp. *tenuifolia*, *A. viridis* ssp. *sinuata*, and *A. oblongifolia*. Both layering and cuttings are effective methods of propagating alders, and submerged branches in nature are sometimes observed with adventitious roots. On the other hand, *Alnus* produces abundant seed (fruits), and one would expect thickets of individual plants to develop in suitable habitats from natural seeding alone. Steele (1961), judging from the amount of variation observed in clumps of *A. incana* ssp. *rugosa* and *A. serrulata*, concluded that these were not clones.

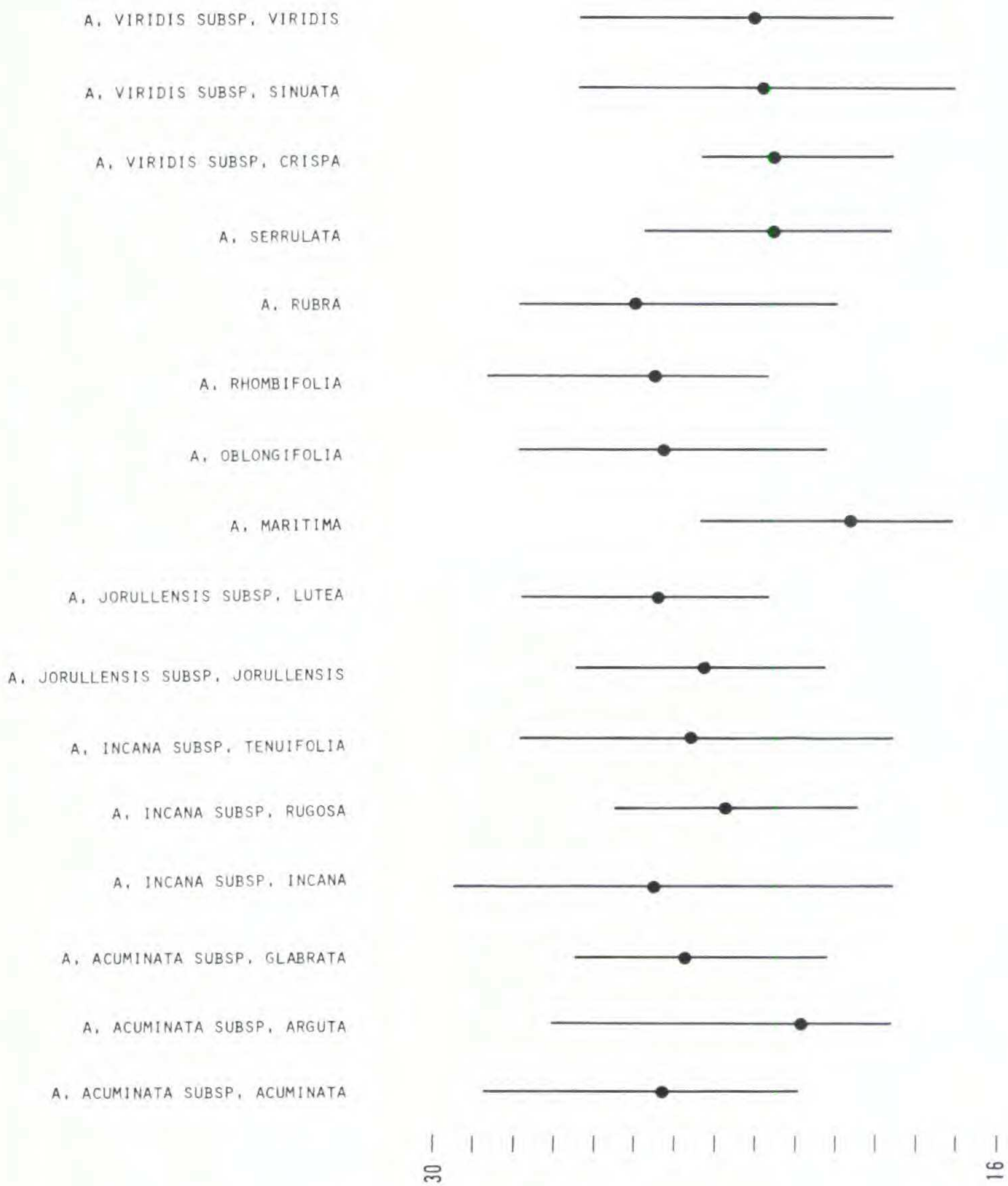


Figure 21. Range of variation in diameter of *Alnus* pollen grains (microns).

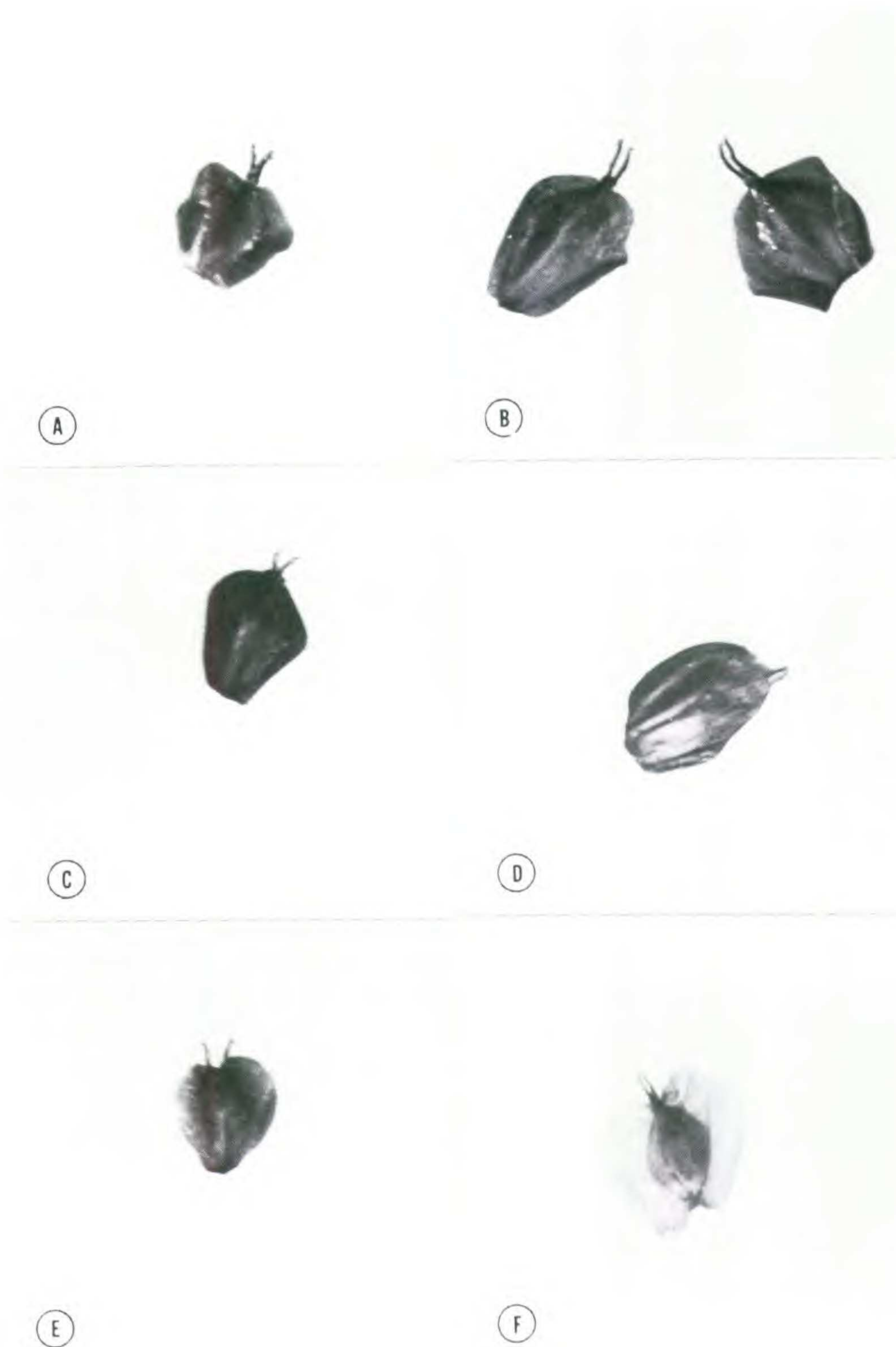


Figure 22. Fruits of representative species of *Alnus*, all ×8. A, *Alnus acuminata* ssp. *acuminata*. B, *A. oblongifolia*. C, *A. incana* ssp. *rugosa*. D, *A. maritima*. E, *A. serrulata*. F, *A. viridis* ssp. *sinuata*.

The fruits of *Alnus* are small and usually winged. Their dispersal in most cases is probably by wind. In some species, however, the wings are much reduced and somewhat corky, apparently serving as floatation mechanisms for water dispersal. McVean (1955) found that the fruits of *A. glutinosa* would float in still water for a period of over 12 months without decomposing. Although no similar study has been made of any of the American species, it seems clear that such essentially wingless-fruited species as *A. maritima* are likewise dispersed mainly by water.

Schalin (1968), using X-ray techniques to determine the developmental stage of the embryo and endosperm in seeds of *Alnus incana* and *A. glutinosa*, found that approximately half of the viable seed contained incompletely-developed embryos. Germination was increased to nearly 100% of viable seed by stratification and cold treatment. This system presumably insures that part of a plant's seed crop will germinate immediately while a portion is delayed until later. Germination in *Alnus* is epigeal and appears to be relatively independent of normal variation in light, temperature, and pH, but it is sensitive to low oxygen and moisture levels (McVean, 1953a).

Many species of *Alnus* hybridize, and numerous putative natural hybrids have been named (Winkler, 1904; Murai, 1964, 1968). Of the New World species, three pairs of taxa have long been suspected of hybridizing naturally. The ranges of *A. incana* spp. *rugosa* and *tenuifolia* overlap in north-central Canada, and the two intergrade morphologically in this region. An extremely variable putative hybrid swarm exists where *A. viridis* spp. *crispa* and *sinuata* occur sympatrically in central and northern Alaska (Hulten, 1944), as does one in the region where *A. incana* ssp. *rugosa* and *A. serrulata* come in contact. In the latter case, Steele (1961) found that hybrids "normally occur in places that may be regarded as somewhat intermediate, and that have almost invariably been disturbed by man" and concludes that *A. serrulata* is introgressing into *A. incana* in this area. No conclusive evidence for hybridization among the various Latin American taxa exists, but the range of variation in some of the species strongly suggests that it does occur. Intermediate forms between *A. acuminata* spp. *arguta* and *glabrata*, between *A. acuminata* ssp. *arguta* and *A. jorullensis*, and between *A. jorullensis* spp. *jorullensis* and *lutea* are rather frequently observed, and these occur in places where hybridization could be expected.

Because putative hybridization is so frequent in the genus, one

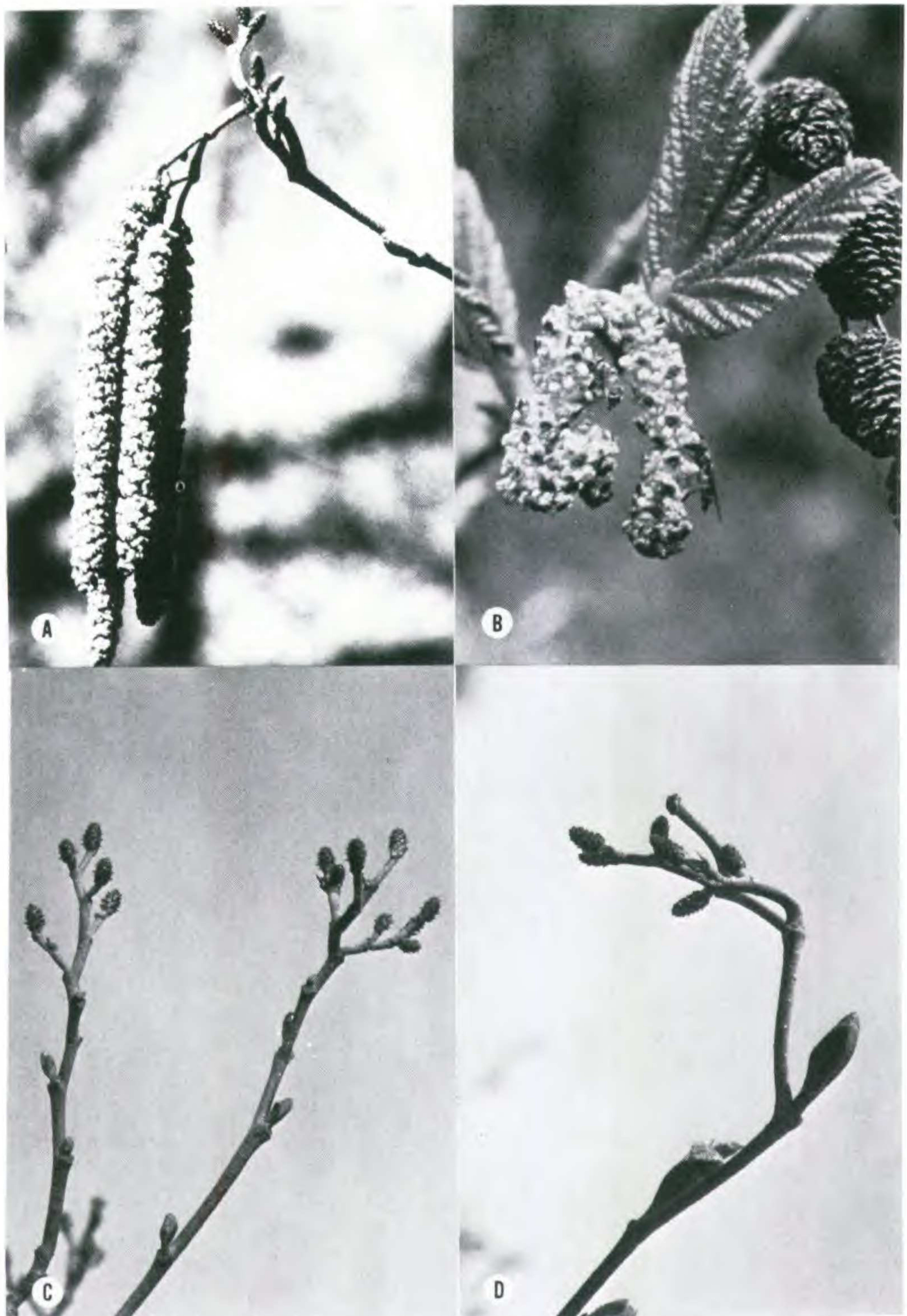


Figure 23. A, pistillate and staminate inflorescences of *Alnus serrulata*. B, syrphid flies visiting staminate catkins of *Alnus viridis* ssp. *crispa* in Terra Nova National Park, Newfoundland (photograph courtesy of Garrett E. Crow). C, pistillate inflorescences of *Alnus serrulata* showing the typical erect axis. D, pistillate inflorescences of *Alnus incana* ssp. *rugosa* showing the typical geniculate axis.

may conclude that reproductive isolation in *Alnus* species is mainly extrinsic in nature. Successful crossing among the three subgenera has not been reported, however. *Alnus maritima* is effectively isolated from all the other species by its flowering season. Several species of the subgenera *Alnus* and *Alnobetula* grow sympatrically, but they do not produce hybrid offspring. Within each subgenus, the species or infraspecific taxa are all separated either geographically or altitudinally and climatically.

Apomixis was described in *Alnus serrulata* from New England by Woodworth (1929, 1930). Meiosis in the plants studied (called *A. rugosa* by the author) was found to be extremely abnormal. Pistillate catkins were found to have no embryo sac development at the time of pollen release, and the pollen was judged to be less than 5% morphologically normal, yet the plants produced an abundance of viable seed. Embryo sac development began about three months after the pollen was shed without a reduction of chromosome number. From one to four embryo sacs developed in each ovule, one to five embryos maturing in each embryo sac. The embryos were seen developing from the diploid egg and by nucellar budding. In a later paper, Woodworth (1931) showed that *A. serrulata* from Virginia produced almost perfect pollen and concluded that the cytological irregularities seen in the New England populations were the result of hybridization with *A. incana* ssp. *rugosa*.

Pollen of specimens selected from throughout the range of each taxon was examined (as described above), but such morphological abnormalities were not found in any other species or in any other part of the range of *Alnus serrulata*. From these results it appears that apomixis is rare or absent in most of the American species of the genus. Further work, especially on a population basis, is needed for a better understanding of this problem.

CHROMOSOME NUMBERS

All of the American species of *Alnus* for which chromosome information is available have numbers of $2n = 28$ (Table 4). Unfortunately, there are no data for *Alnus rhombifolia*, *A. oblongifolia*, nor for any of the Latin American taxa.

In 1934, Wanscher predicted that the basic chromosome number in the Betulaceae is $x = 7$, based on numbers of $x = 8$ in *Carpinus* and *Ostrya* and $x = 14$ or higher in the other genera. In 1962, Chiba

found a diploid number of 14 in root tip cells of Japanese *Alnus hirsuta* var. *microphylla* (*A. inokumae* Murai & Kusaka), a taxon which may be conspecific with *A. incana*. In the typical variety of *A. hirsuta*, the number was found to be $2n = 28$. The basic chromosome number in *Alnus* is therefore taken to be $x = 7$.

Four levels of polyploidy occur in *Alnus*, although $2n = 28$ is by far the most common condition. In addition to the number reported by Chiba ($2n = 14$) and the many species having $2n = 28$, several European and Asian species have numbers of $2n = 42$ and $2n = 56$. *Alnus glutinosa* has been reported with somatic chromosome numbers of both $2n = 28$ and $2n = 56$ (Woodworth, 1929, 1931), while *A. subcordata* and *A. japonica* may have either $2n = 28$, $2n = 42$, or $2n = 56$ (Gram *et al.*, 1941; Jaretzky, 1930; Woodworth, 1929, 1931). *Alnus cordata* has been found with either $2n = 28$ or $2n = 42$ (Jaretzky, 1930). *Alnus orientalis* has been found with $2n = 42$ (Gram *et al.*, 1941). In addition, Kodama (1967) reported a chromosome number of $2n = 112$ from root nodule tissue of *Alnus firma* in Japan, but it is not known whether other parts of the plant had this number.

Jaretzky (1930) and Gram *et al.* (1941) report that meiosis is irregular and the pollen quality poor in the species having 42 chromosomes (*Alnus cordata*, *A. subcordata*, and *A. orientalis*). In plants having $2n = 56$ chromosomes, meiosis is nearly regular and almost all the pollen is well-formed (Gram *et al.*, 1941). All reports for species in which $2n = 28$ (except those involving putative hybrids between *A. incana* ssp. *rugosa* and *A. serrulata* by Woodworth, 1929, 1930, 1931) likewise indicate a normal meiosis.

It seems clear that the alders with chromosome numbers of $2n = 28$ and $2n = 56$ represent a simple polyploid series. Those with 42 chromosomes may have resulted from hybridization between $2n = 28$ and $2n = 56$ types.

PHYLOGENETIC TRENDS

Divergence and Convergence. From anatomical evidence (Tippo, 1938; Hall, 1952) the Betulaceae are not primitive but are regarded as low in the Amentiferae. Tippo considers *Betula* and *Alnus* to be the most primitive genera, *Corylus* and *Ostryopsis* less so, and *Carpinus* and *Ostrya* least primitive. Within *Alnus* itself, consider-

able morphological and biochemical variation suggests extensive specialization and divergence among various species and groups of species.

Table 4. Chromosome numbers reported for American species of *Alnus* and their Eurasian vicariants.

Species	Number (2n)	Reference
<i>A. incana</i> ssp. <i>incana</i>	28	Gram, et. al., 1942
	28	Löve, 1954
	28	Wetzel, 1928
<i>A. incana</i> ssp. <i>rugosa</i>	28	Löve, 1954
	28	Woodworth, 1929
	28	Woodworth, 1931
<i>A. incana</i> ssp. <i>tenuifolia</i>	28	Gram, et al., 1942
<i>A. maritima</i>	28	Wetzel, 1929
	28	Woodworth, 1929
	28	Woodworth, 1931
<i>A. rubra</i>	28	Taylor & Mulligan, 1968
	28	Gram, et al., 1942
	28	Jaretsky, 1930
	28	Wetzel, 1927
	28	Wetze, 1928
<i>A. serrulata</i>	28	Woodworth, 1929
	28	Woodworth, 1930
	28	Woodworth, 1931
<i>A. viridis</i> ssp. <i>crispa</i>	28	Löve, 1954
	28	Löve & Löve, 1965
	28	Löve & Löve, 1966
	28	Pouques, 1949
	28	Woodworth, 1929
	28	Woodworth, 1931
<i>A. viridis</i> ssp. <i>sinuata</i>	28	Taylor & Mulligan, 1968
	28	Löve, 1954
<i>A. viridis</i> ssp. <i>viridis</i>	28	Contandriopoulos, 1964
	28	Jaretsky, 1930
	28	Pouques, 1949
	28	Wetzel, 1928
	28	Wetzel, 1929

At the infrageneric level, the alders have diverged into three distinct groups, treated here as the subgenera *Alnus*, *Alnobetula*, and *Clethropsis*. Subgenus *Alnobetula* is adapted to a cold environment, as shown by its present distribution in the boreal latitudes and at high elevations, and by morphological features including the shrub habit and reduction in the size of many structures. At the same time, several other characters, such as the presence of long peduncles, appear to remain primitive in the subgenus.

The basic morphological pattern seen in the "primitive" members of subgenus *Alnus* (illustrated best in America by *A. rubra*, *A. oblongifolia*, and *A. acuminata*) suggests adaptation to a mesic, temperate existence. The Latin American members of this subgenus have diverged from this pattern to a greater or lesser extent, being adapted to a somewhat warmer climate with rainy and dry seasons. None becomes dormant for an extended period as do their northern relatives. One species of this group (*A. jorullensis*) has gained the ability to exist in drier and colder habitats. Individuals of this taxon often have thicker, smaller leaves, thicker bark, and other characters suggesting adaptation to more xeric conditions. *Alnus serrulata* and *A. rhombifolia* of the southern United States have also diverged in this direction and possess many of the same specializations. *Alnus incana*, like *A. viridis*, has become adapted to a cool environment, but not to the same extent. Here may be seen convergence in such characters as the shrub habit and smaller leaves, while the subgeneric characteristics (e.g., the pistillate catkins exposed during the winter before anthesis) are retained.

Although some phylogenetic taxonomists have concluded that subg. *Clethropsis* represents the most primitive segment of the genus (Takhtajan, 1960; Murai, 1964), *Alnus maritima* is seen to possess a host of apparently derived characters, including reduced fruit wings, a semi-shrub habit, autumn flowering, reduced inflorescences, and relatively small obovate leaves. Its peculiar geographical distribution in America suggests great antiquity, but it is not primitive morphologically, at least in readily-observable characters, when compared with such species as *A. oblongifolia*, *A. rubra*, and *A. acuminata*.

Three American species of *Alnus* are represented regionally as subspecies. In each of these, the subspecies have diverged, but they intergrade where their ranges overlap. The strongest divergence occurs in *A. viridis* spp. *crispa* and *sinuata*, ssp. *crispa* being better adapted to low elevations and ssp. *sinuata* to montane conditions;

both are more or less flexible in this respect (ssp. *sinuata* also sometimes occurring in moderate lowland regions along the Pacific coast and ssp. *crispa* sometimes occurring in rather severe montane conditions in the East). There is less morphological differentiation between the subspecies of *A. incana*, although ssp. *rugosa* is shrubbier in habit than ssp. *tenuifolia* (apparently a derived state since the other subspecies of *A. incana* are all more treelike). *Alnus acuminata* has diverged to a lesser extent than *A. viridis* and *A. incana* in North and South America, and it has not adopted a radically different habitat in either area, probably because the two populations have been separated only since the Pleistocene.

Alnus is an old genus, and convergence has apparently occurred repeatedly in many characters. This is especially true for some of the easily-seen features by which the species are recognized in the field (habit, leaf shape, pubescence, and cone size), and in most cases, the specializations have developed under similar environmental conditions where they have appeared in two or more otherwise distinct species. Similar phenomena have been described in many other temperate woody genera, most recently by Tucker (1974) in the genus *Quercus*.

Phylogeny. The relatively large amount of convergence in *Alnus*, together with its wide distribution and apparent repeated migrations over a long period of time make the construction of a phylogeny difficult. However, certain patterns are repeated in the results of the various studies reported here. A phylogenetic tree, synthesized from all of this data, is provided in Figure 24. The base of this figure represents the supposed origin of the genus, and the tips of the branches the present American species and subspecies, together with the Eurasian vicariants of American taxa. Taxa toward the center of the tree are regarded as relatively unspecialized, while those away from the center are seen as more advanced, though in a few cases it was not possible to accurately represent the taxa in this way and still show their true cladistic relationship (e.g., in the case of *A. rhombifolia*, *A. oblongifolia*, and *A. acuminata*). While they represent progressive development in a qualitative sense, neither the horizontal nor the vertical axis is intended to indicate relationship or time quantitatively. Because extinction has certainly occurred many times in the genus, there are bound to be gaps and missing branches, and because the tree is necessarily drawn in only two



Figure 24. Phylogenetic tree of the New World taxa of *Alnus* and their Eurasian vicariants.

dimensions, some additional distortion has to be present. Nevertheless, this scheme provides an approximate picture of the relationships among the present taxa of North and South America based on the present study.

ECONOMIC IMPORTANCE

Alnus has long been used by man, especially for lumber, in tanning and dyeing, for the production of charcoal, and as an astringent medication. It was important to the ancient Greeks and Romans for shipbuilding, and medieval builders, seeing that alders grew near water, concluded that the wood of this tree must be resistant to moisture and constructed much of Venice and Amsterdam on piles made from its trunks.

Among the more obscure uses for alders is one reported by Nicholas Culpeper in 1653, who writes that "leaves gathered while the morning dew is on them, and brought into a chamber troubled with fleas, will gather them thereonto, which being suddenly cast out, will rid the chamber of those troublesome bedfellows." Coon (1963) states that "the twigs, bark, and catkins are a source of a black dye that has been known and used for centuries. Used alone, it dyes wool a reddish color and used with copperas, produces a good black. Young shoots produce colors from yellow to cinnamon, while the leaves will produce a dye for leather." Other uses of *Alnus* in Europe, including the manufacture of wooden shoes and clog soles, are reviewed by Eldin (1964).

Although seldom a major timber source in America, *Alnus* is nevertheless important for a variety of wood products. In the Pacific Northwest the wood of *Alnus rubra* is used in cabinetry as well as for the manufacture of toys, trays, brush handles, spools, shoe soles, boxes, and other small items (cf. Worthington *et al.*, 1962). It is also an important source of pulp for paper in this region, and research into its productivity, management, etc. has been increasing in recent years (cf. Smith, 1968; Williamson, 1968). *Alnus acuminata* finds similar uses throughout its range from Mexico to Argentina. Acosta-Solis (1939) states that in Ecuador alder wood "is used in carpentry, furniture making, and cabinet work, and before Eucalypt lumber became available, was employed in general construction in the same way as Calupf, Sauce, Algarrobo, and Arrayan. In the province of Tungurahua it is used for making the boxes and packing cases in which fruit is exported."

Commenting on the shrubby stature of the alders of eastern North America, Michaux (1859) states that "common alder¹ is too small to be applicable to any use in the arts: from its inferiority of size, it will probably one day give place to the European Alder" and "the dwarfish stature of all the species of Alder that have hitherto been discovered in North America excludes them from that class of vegetation to the description of which I have restricted my labors; but I could not forbear mentioning the two most remarkable species, of which one² merits attention on account of its abundant diffusion, and the other³ on account of a striking peculiarity in the color of its leaves." In spite of their small size, even the shrubby alders of the New World have important uses. Among these is their use as a source of firewood for the natives of regions where other fuels are scarce, including parts of Alaska (Porsild, 1939) and the high Andes of South America (Record & Hess, 1943).

The ability of alders to fix atmospheric nitrogen may someday benefit the forestry industry. According to Tarrant (1968), "evidence from many studies indicates that alder (*Alnus* spp.) has a potential relation to forestry similar to that of legumes to Agriculture." Presently, however, members of the genus have not found extensive use in this way in North America.

The bark and foliage of *Alnus* are very astringent and are used in primitive American societies for medicinal purposes. Smith (1923, 1928, 1932, & 1933) reports a number of such uses among American Indians, including the making of poultices to reduce swellings and infusions or teas to treat sores, the passing of blood in stools, cases of piles, and the flux. He (1923) states that "the white man has held valuable its astringent properties in the treatment of diarrhea and haematuria. The liquid has been used as a mouth wash or gargle in the treatment of stomatitis and pharyngitis. When injected into the vagina, it is said to cure leucorrhoea." Standley (1920) mentions that in Mexico an infusion of bark is used as a lotion for cutaneous diseases and that a decoction of the bark is sometimes taken internally for scrofula and venereal diseases. Martinez (1959) reports that the bark of *A. firmifolia* (= *A. jorullensis*) is sold in Mexican markets for such purposes. In Peru, the leaves of alders are crushed

¹*Alnus serrulata*.

²*Alnus serrulata*.

³*Alnus incana* ssp. *rugosa*.

with butter to cicatrize wounds and also used without fat to protect against inflammation. Applied to recent wounds, the leaves are used to stop bleeding (Macbride, 1936). In the United States, according to Vines (1960), the bark of *A. serrulata* was formerly used in the treatment of "intermittent fever". Smith (1932) states that "the eclectic practitioner in the United States and Canada employed it [the bark] in a powdered condition for dusting upon chafed body surfaces."

Other native American uses of the alders include the tanning and dyeing of leather and textiles with preparations of the bark (Macbride, 1936; Smith, 1923, 1932, & 1933; Standley, 1920; Standley & Steyermark, 1952). In some regions alders are of limited value for livestock forage. All of the species are important in the reduction of soil erosion since *Alnus* is among the first of the colonizers to follow fires, lumbering, volcanic eruptions, and other disturbances of the natural vegetation. In Great Britain, the Netherlands, and Germany, alders have been used for some time in the rehabilitation of mine spoils (Tarrant, 1968).

SPECIMENS EXAMINED

Approximately 9,000 specimens were examined during this study. In the treatment of each taxon on the following pages, only representative specimens are cited, but the collection sites of all the material seen have been plotted on the maps. The specimens cited were chosen for use in the numerical taxonomic part of the work and represent the complete range of phenotypic and geographical variation observed. A list of all the specimens used has been prepared and placed on file in the Beal-Darlington Herbarium of Michigan State University. This is also available to interested individuals from the author.

In the citation of specimens, herbaria have been given the abbreviations used in the sixth edition of *Index Herbariorum* (Holmgren & Keuken, 1974). Collections from the following institutions were examined: The Arnold Arboretum, Harvard University (A); The University of Alberta (ALTA); The University of Arizona (ARIZ); The National Museum of Canada (CAN); Biosystematics Research Institute, Canada Department of Agriculture (DAO); The Dudley Herbarium, Stanford University (DS); Herbario de la Escuela Nacional de Ciencias Biologicas, Instituto Polytécnico

Nacional, México (ENCB); The Searle Herbarium, Field Museum of Natural History (F); The Gray Herbarium, Harvard University (GH); Indiana University (IND); The Jepson Herbarium, The University of California (JEPS); Herbario Nacional del Instituto de Biología de la Universidad Nacional Autónoma de México (MEXU); The University of Michigan (MICH); The Missouri Botanical Garden (MO); The Beal-Darlington Herbarium, Michigan State University (MSC); The University of Notre Dame (ND); The Greene Herbarium, The University of Notre Dame (NDG); The New England Botanical Club Herbarium (NEBC); The New York Botanical Garden (NY); The Bebb Herbarium, The University of Oklahoma (OKL); The Ohio State University (OS); The University of Pennsylvania (PENN); The Academy of Natural Sciences of Philadelphia (PH); The Rocky Mountain Herbarium, The University of Wyoming (RM); The University of California at Berkeley (UC); United States National Herbarium, Smithsonian Institution (US); The University of Wisconsin (WIS); The University of Washington (WTU).

TAXONOMIC TREATMENT

Alnus P. Miller, Gard. Dict., Abbr. ed. 4. 1754.

Alnus Tournefort, Inst. Rei Herb. 1: 587. 1700; Ehrhart, Oekon. Pfl. Hist. 2: 211. 1753; Miller, Gard. Dict., Abbr. ed. 4. 1754.

Betula Linnaeus, Sp. Pl. 2: 983. 1753, in part as to species 5.

Betula-alnus Weston, Bot. Univers. Hortul. 1: 1770, not validly published.

Betula-alnus Marshall, Arb. Amer. p. 20. 1785, *nom. illeg.*

Deciduous monoecious trees and shrubs with narrowly to broadly ovate to obovate leaves, watery sap, smooth to (in age) scaly astringent bark, and terete branchlets with triangular pith and (usually) conspicuous circular to elliptic lenticels, the twigs, buds, and foliage sparsely to densely covered with simple straight hairs and minute peltate glands; sapwood white, soft, close, straight-grained, and brittle, becoming red when exposed to the air before dry; heartwood reddish-brown, usually forming only a small core; roots often stoloniferous, the rootlets fibrous, bearing nodules containing nitrogen-fixing endophytes. Leaf buds with 2 or 3 equal mostly valvate stipular scales or 5 or more imbricate scales, raised on well-defined minute stems (stipitate), elongate, often slightly three-angled, ovoid to oblong and acuminate, acute, or rounded at

the apex, resin-coated; apical bud pseudoterminal. Leaves alternate, simple, pinnately-veined, singly- or doubly-serrate to nearly entire, petiolate, deciduous, shed while still green; in the bud enclosed in their stipules, becoming conduplicate in expansion, plicately-folded along the lateral veins. Leaf scars often elevated, obtuse to rounded below and somewhat notched above, with three large approximately equidistant circular to crescent-shaped bundle scars, the lowest often obviously composed of three smaller scars. Stipules ovate, elliptic, or obovate, acute to rounded at the apex, glandular, glabrous to densely pubescent, ciliate-margined, deciduous or moderately persistent. Flowers unisexual, sessile, in modified cymules reduced and arranged into pedunculate bracteate aments, the peduncles from the axils of leaves or minute leafy bracts, opening in the early spring before or with the unfolding of the leaves, or in later summer or autumn, often partially developed during the previous growing season and either exposed or enclosed in the bud during dormancy. Pistillate inflorescences ovoid to oblong or cylindric, erect, pedunculate, formed in the axils of the leaves of a branchlet developing in the axil of one of the upper leaves on the main axis below the staminate inflorescences, appearing as a racemose cluster or solitary on the main stem; bracts subtended by and adnate with 4 bracteoles, imbricate, and somewhat fleshy. Pistillate flowers 2 per bract, without perianth. Pistil 1, compressed, 2- (or rarely 3-) carpellate; ovary inferior, 2- (rarely 3-) locular below and 1-locular above; ovules 2, one per locule, axially attached near the summit of the locule, pendulous, anatropous; styles 2, linear, free, each stigmatic near the apex. Pistillate inflorescences enlarging, the bracts becoming thick and woody after anthesis; mature scales obovate, 3- to 5-lobed or truncate at the apex, forming a persistent subglobose, ovoid, or cylindric strobilus-like infructescence. Staminate catkins elongate, pendulous, in one or more racemose clusters or solitary in the axils of leaves or leafy bracts; bracts short-stalked, peltate, adnate at the base to 3 or 5 bracteoles, subtending 3 (to rarely 6) minute flowers. Perianth of one series, 4- (or infrequently 1- to 6-) parted, the segments ovate, elliptic, or obovate and connate at the base, glandular-margined; stamens 2 or 4 (occasionally 5 or 6), short (never much exerted from the catkin), inserted at the base of the perianth parts and often basally adnate to them; filaments short to long, undivided; anthers erect, dorsifixed, introrse, 4-sporangiate and 2-locular, the thecae parallel, partially

separate, contiguous, dehiscing longitudinally. Fruit a small, flattened, ovate, elliptic, orbicular, or obovate nutlet or samara, pointed and crowned at the apex by the remnants of the styles, wingless (with a narrow wing-like chartaceous border) or broadly membranaceous winged on 2 margins; pericarp of 2 coats, the outer thin and membranaceous, the inner thick and crustaceous. Seed solitary by abortion, filling the cavity of the fruit, the hilum apical, testa membranaceous, without endosperm. Embryo large, straight, the radicle superior and shorter than the flat, fleshy cotyledons.

LECTOTYPE SPECIES: *Alnus glutinosa* (Linnaeus) Gaertner (*Betula alnus* α *glutinosa* Linnaeus).

Alnus is the classical Latin name for the alder tree and for objects made from its wood, including ships and boats. In this connection it was used by Virgil, Pliny, and others. It is presumably derived from the Latin verb *alo* (to nourish), referring to its usual close association with water.¹ The English name *alder* is derived from the Old English *alor*, *aler* (Murray *et al.*, 1933).

The genus was generally considered distinct from *Betula* until the two were combined as *Betula* by Linnaeus in *Species Plantarum* (1753). Phillip Miller was the first to resurrect *Alnus* in the *Gardner's Dictionary, Abridged*, ed. 4 (1754), but since he did not use binomial nomenclature one of his species cannot be designated the type. In the 8th edition of the *Gardner's Dictionary* (1768), where he first used binomials, Miller omitted the genus altogether, apparently partly by mistake, referring the reader first under "Alder-Tree" to *Alnus*, and then under "*Alnus*" to *Betula*, but not including any alder species there. The first treatment employing binomial nomenclature to list *Alnus* species, excluding Hill's *The British Herbal* of 1757 because of its inconsistency in the use of binomials (cf. Stafleu *et al.*, 1972), is Gaertner's *De Fructibus et Seminibus Plantarum* (1790). The only species of *Alnus* cited in this work is *A. glutinosa* (Linnaeus) Gaertner, based on Linnaeus' *Betula alnus* α *glutinosa* (Sp. Pl. 2: 983. 1753). This species has therefore been chosen as the lectotype of the genus.

¹Wood (1880) states that the Latin name is derived from the Celtic *al* (near) and *lan* (riverbank), also referring to its usual habitat.

ARTIFICIAL KEY TO THE SUBGENERA, SPECIES, AND
INFRA-SPECIFIC TAXA

1. Winter buds stalked, covered (sometimes incompletely) by 2 or 3 equal stipular scales; leaf-bearing stems usually not forming both long and short shoots; staminate and pistillate inflorescences produced mid to late in the growing season, not with new growth in the spring. 2.
2. Lateral veins of the leaves terminating in teeth at the margin; pistillate inflorescences (and later infructescences) borne on short branchlets in racemose clusters; flowering occurring at the beginning of the growing season (spring). Subg. *Alnus*. 3.
3. Leaves mostly ovate (rarely elliptic), finely serrate or serrulate to rather coarsely double-serrate. 4.
4. Leaf margins finely and evenly serrate or serrulate, sometimes slightly lobed; trees of the western United States. ... 3. *A. rhombifolia*.
4. Leaf margins serrate or double-serrate to irregularly-toothed.. 5.
5. Margin of leaf blade strongly revolute; large trees of north-western coastal North America. 1. *A. rubra*.
5. Margin of leaf blade flat or only slightly to moderately revolute; trees and shrubs. 6.
6. Leaves lanceolate to narrowly ovate or ovate. 7.
7. Major teeth of the leaves sharp and acuminate, usually standing out well above the secondary teeth. 8.
8. Internodes, petioles, and lower leaf surfaces and veins glabrous; staminate flowers with 4 stamens and perianth parts; trees of central and southern Mexico. 4c. *A. acuminata* ssp. *glabrata*.
8. Internodes, petioles, and lower leaf surfaces and veins at least sparsely pubescent, often villous to velutinous; staminate flowers with either 2 or 4 stamens and perianth parts. 9.
9. Stamens and perianth parts 4, equal in size; trees of South America.
..... 4a. *A. acuminata* ssp. *acuminata*.
9. Stamens and perianth parts 2 or 4, if 4, then 2 large and 2 smaller; trees of the southwestern United States and adjacent northern Mexico.
..... 2. *A. oblongifolia*.
7. Major teeth of the leaves acute to obtuse, short to long.
..... 2. *A. oblongifolia*.
6. Leaves moderately to broadly ovate, the major teeth obtuse to rounded. 10.
10. Leaves usually large, the blade 5–19 cm long, relatively finely double-serrate or serrate, the apex usually acuminate, densely glandular below; infructescences 11–45 mm long; bark usually with transverse constrictions or ridges; trees of Mexico, Central America, and South America. 11.

11. Leaves usually finely serrate or serrulate; trees of South America. 4a. *A. acuminata* ssp. *acuminata*.
11. Leaves usually double serrate; trees of Mexico and Central America. 4b. *A. acuminata* ssp. *arguta*.
10. Leaves usually smaller, the blade 4–10 cm long, more coarsely double-serrate, the apex usually acute to obtuse, sparsely to only moderately glandular below; infructescences 10–17 mm long; bark without transverse constrictions; large shrubs and small trees of Canada and the northern and western United States. 12.
12. Leaf blade moderately thick, the major teeth acute; large shrubs of eastern Canada and the northeastern United States. 6a. *A. incana* ssp. *rugosa*.
12. Leaf blade thin and papery, the major teeth usually rounded; large shrubs or small trees of the western United States and Canada. 6b. *A. incana* ssp. *tenuifolia*.
3. Leaves mostly elliptic, oblong-elliptic, or obovate, occasionally tending toward ovate. 13.
13. Leaves more or less orbicular, the apices usually retuse (occasionally rounded); moderately large trees naturalized in the northeastern United States and adjacent Canada. 8. *A. glutinosa*.
13. Leaves ovate, elliptical, oblong, or obovate, the apices acute to obtuse or sometimes slightly rounded; trees and shrubs of the United States, Canada, Mexico, and Central America. 14.
14. Leaf margins finely and evenly serrulate; leaf texture papery to moderately coriaceous. 15.
15. Leaf blades broadly elliptic to obovate, the apices often more or less rounded; staminate flowers with 4 stamens; large shrubs of eastern North America. . 7. *A. serrulata*.
15. Leaf blades narrowly elliptic or rhombic, the apices usually not rounded; stamens 2 (or 4 with 2 reduced in size); large trees of the western United States. . . 3. *A. rhombifolia*.
14. Leaf margins rather coarsely and unevenly toothed or wavy, especially near the apex; leaf texture very firm and leathery; large trees of southern Mexico and Guatemala. 16.
16. Lower leaf surface with relatively few small widely-spaced whitish, yellowish, or brownish glands. 5a. *A. jorullensis* ssp. *jorullensis*.
16. Lower leaf surface densely covered with large whitish to bright yellow glands. 5b. *A. jorullensis* ssp. *lutea*.
2. Lateral veins of the leaves usually terminating by anastomosing with other veins near the margin (infrequently ending in the teeth); pistillate inflorescences (and later infructescences) solitary in leaf axils along the main stems; flowering occurring near the end of the growing season (late summer or autumn). Subg. *Clethropsis*. 10. *A. maritima*.

1. Winter buds sub-sessile (stalks not over 1 mm long), covered by 5 or more unequal imbricate scales; leaf-bearing stems usually with both long shoots and short spurs, the latter bearing the leaves; staminate inflorescences produced late in the previous growing season, pistillate inflorescences produced along with the first new growth of the season. Subg. *Alnobetula*. 17.
17. Leaves finely serrate or serrulate (rarely double-serrate), leathery, dark green, and sometimes sparsely to densely pubescent below; shrubs of the eastern United States and adjacent Canada, northern Canada to Alaska, and the Pacific coast south to northern California.
 9a. *A. viridis* ssp. *crispa*.
17. Leaves moderately to coarsely double-serrate (rarely singly or finely serrate), thin to membranaceous, light or yellowish green, glabrous; shrubs of the mountainous and coastal western United States and Canada.
 9b. *A. viridis* ssp. *sinuata*.

Alnus* Miller subg. *Alnus

- Alnus* Miller, Gard. Dict., Abbr. ed. 4 1754; *Alnus* c. *Alnus* Endlicher, Gen. Pl. suppl. 2, p. 28. 1842; *Alnus* sect. *Alnus* Sargent, Silva North Amer. 9: 68. 1896; *Alnus* subg. II. *Alnus* Schneider in Sargent, Pl. Wilson. 2(3): 490. 1916.
- Alnus* sect. II. *Clethra* W. D. J. Koch, Syn. Fl. Germ. Helvet., p. 663. 1837. LECTOTYPE: *A. glutinosa* (Linnaeus) Gaertner.
- Alnus* sect. II. *Gymnothyrsus* Spach, Ann. Sci. Nat. ser. 2, 15: 204. 1841; *Alnus* IV. subgen. *Gymnothyrsus* (Spach) Regel, Bull. Soc. Nat. Mosc. 38(3): 425. 1865. LECTOTYPE: *A. glutinosa* (Linnaeus) Gaertner.
- Alnus* sect. I. *Phyllothyrsus* Spach, Ann. Sci. Nat. ser. 2, 15: 204. 1841; *Alnus* sect. *Gymnothyrsus* subsect. *Phyllothyrsus* (Spach) Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. 17: 98. 1955. LECTOTYPE: *A. acuminata* Humboldt, Bonpland, & Kunth.
- Alnus* subgen. *Euclethrus* Petermann, Deutschl. Fl. p. 516. 1849. LECTOTYPE: *A. glutinosa* (Linnaeus) Gaertner.
- Alnus* sect. II. *Betulaster* Regel, Mem. Soc. Nat. Mosc. 13(2): 144. 1861. TYPE: *A. lindeni* Regel (= *A. acuminata* Humboldt, Bonpland, & Kunth).
- Alnus* sect. IV. *Eualnus* Regel, Mem. Soc. Nat. Mosc. 13(2): 152. 1861. LECTOTYPE: *A. glutinosa* (Linnaeus) Gaertner.
- Alnus* sect. III. *Pseudalnus* Regel, Mem. Soc. Nat. Mosc. 13(2): 145. 1861. LECTOTYPE: *A. acuminata* Humboldt, Bonpland, & Kunth.
- Alnus* sect. *Pycnantha* Muller, Madroño 5: 152. 1940. TYPE: *A. densiflora* Muller (= *A. incana* (Linnaeus) Moench).
- Alnus* sect. *Gymnothyrsus* subsect. *Hedroiostachys* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. 17: 101. 1955. TYPE: *A. glabrata* Fernald (= *A. acuminata* Humboldt, Bonpland, & Kunth).
- Alnus* sect. *Gymnothyrsus* subsect. *Phyllothyrsus* ser. *Acutissimae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. 17: 99. 1955. TYPE: *A. acutissima* (Winkler) Callier (= *A. acuminata* Humboldt, Bonpland, & Kunth).
- Alnus* sect. *Gymnothyrsus* subsect. *Phyllothyrsus* ser. *Ferrugineae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. 17: 99. 1955. TYPE: *A. ferruginea* Humboldt, Bonpland, & Kunth (= *A. acuminata* Humboldt, Bonpland, & Kunth).

- Alnus* sect. *Gymnothyrsus* subsect. *Podostachys* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 99. 1955. TYPE: *A. serrulatoides* Callier.
- Alnus* sect. *Gymnothyrsus* subsect. *Podostachys* ser. *Glutinosae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 100. 1955. TYPE: *A. glutinosa* (Linnaeus) Gaertner.
- Alnus* sect. *Gymnothyrsus* subsect. *Podostachys* ser. *Jorullenses* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 101. 1955. TYPE: *A. jorullensis* Humboldt, Bonpland, & Kunth.
- Alnus* sect. *Gymnothyrsus* subsect. *Podostachys* ser. *Rhombifoliae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 100. 1955. TYPE: *A. rhombifolia* Nuttall.
- Alnus* sect. *Gymnothyrsus* subsect. *Podostachys* ser. *Rubrae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 100. 1955. TYPE: *A. rubra* Bongard.
- Alnus* sect. *Proskeimostemon* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 102. 1955. TYPE: *A. hirsuta* Turczaninov (= *A. incana* (Linnaeus) Moench).
- Alnus* sect. *Proskeimostemon* ser. *Incanae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 104. 1955. TYPE: *A. incana* (Linnaeus) Moench.
- Alnus* sect. *Proskeimostemon* ser. *Hirsutae* Czerepanov, Notul. Syst. Herb. Inst. Bot. Kom. Acad. Sci. U.R.S.S. **17**: 103. 1955. TYPE: *A. hirsuta* Turczaninov (= *A. incana* (Linnaeus) Moench).
- Alnus* sect. *Glutinosae* Murai, Bull. Gov. For. Expt. Sta. Jap. **154**: 63. 1963, *nom. nud.*; *Alnus* subgen. *Gymnothyrsus* sect. *Glutinosae* Murai, Bull. Gov. For. Expt. Sta. Jap. **154**: 67. 1963, *pro. syn.*; *Alnus* subgen. *Gymnothyrsus* sect. *Glutinosae* Murai, Bull. Gov. For. Expt. Sta. Jap. **171**: 50. 1964, not validly published.
- Alnus* sect. *Maritimae* Murai, Bull. Gov. For. Expt. Sta. Jap. **154**: 66. 1963, not validly published; *Alnus* subgen. *Gymnothyrsus* sect. *Maritimae* Murai, Bull. Gov. For. Expt. Sta. Jap. **154**: 66. 1963, *pro syn.*

Large shrubs and small to large trees; twigs and young branches not differentiated into long and short shoots; bud stalks well developed; buds covered by 2 (or sometimes 3) equal stipular valvate scales. Leaves coarsely to very finely double-serrate or serrulate; lateral veins ending in major teeth at the margin. Pistillate inflorescences borne on short, stout peduncles, usually without subtending leaves, in racemose clusters on short branchlets along a major branch, the latter bearing the staminate catkins at the upper nodes, usually without subtending leaves, in one or more racemose clusters. Pistillate and staminate inflorescences both formed during the previous growing season and exposed during the dormant period (where present); anthesis occurring in the spring before new growth

commences; fruits maturing at the end of the current growing season; staminate flowers with 4 (occasionally 2) stamens; perianth parts 4, 2 sometimes reduced in size. Fruits lacking wings or merely narrowly wing-margined on two sides.

1. *Alnus rubra* Bongard

Alnus rubra Bongard, Mem. Acad. Sci. St. Petersb. ser. 6, **2**: 162. 1833; *Alnus incana* η *rubra* (Bongard) Regel, Mem. Soc. Nat. Mosc. **13**(2): 157. 1861. TYPE: *Mertens*, "a l'île de Sitcha" (LE?, not seen).

Alnus castaneaefolia Douglas ex Hooker, Fl. Bor. Amer. **1**: 158. 1838, *non* Mirbel, Mem. Mus. Hist. Nat. **14**: 463. 1827, *pro syn.*

Alnus oregona Nuttall, North Amer. Sylva **1**: 44. 1842. TYPE: *Nuttall s.n.*, "on the borders of the rivers Boisée and Brulée, which pass into the Shoshonée not far from Walla-Walla, and at intervals it continues more or less common to Point Chinkook, near the shores of the Pacific" (Holotype, BM?, not seen; Isotype, PH!).

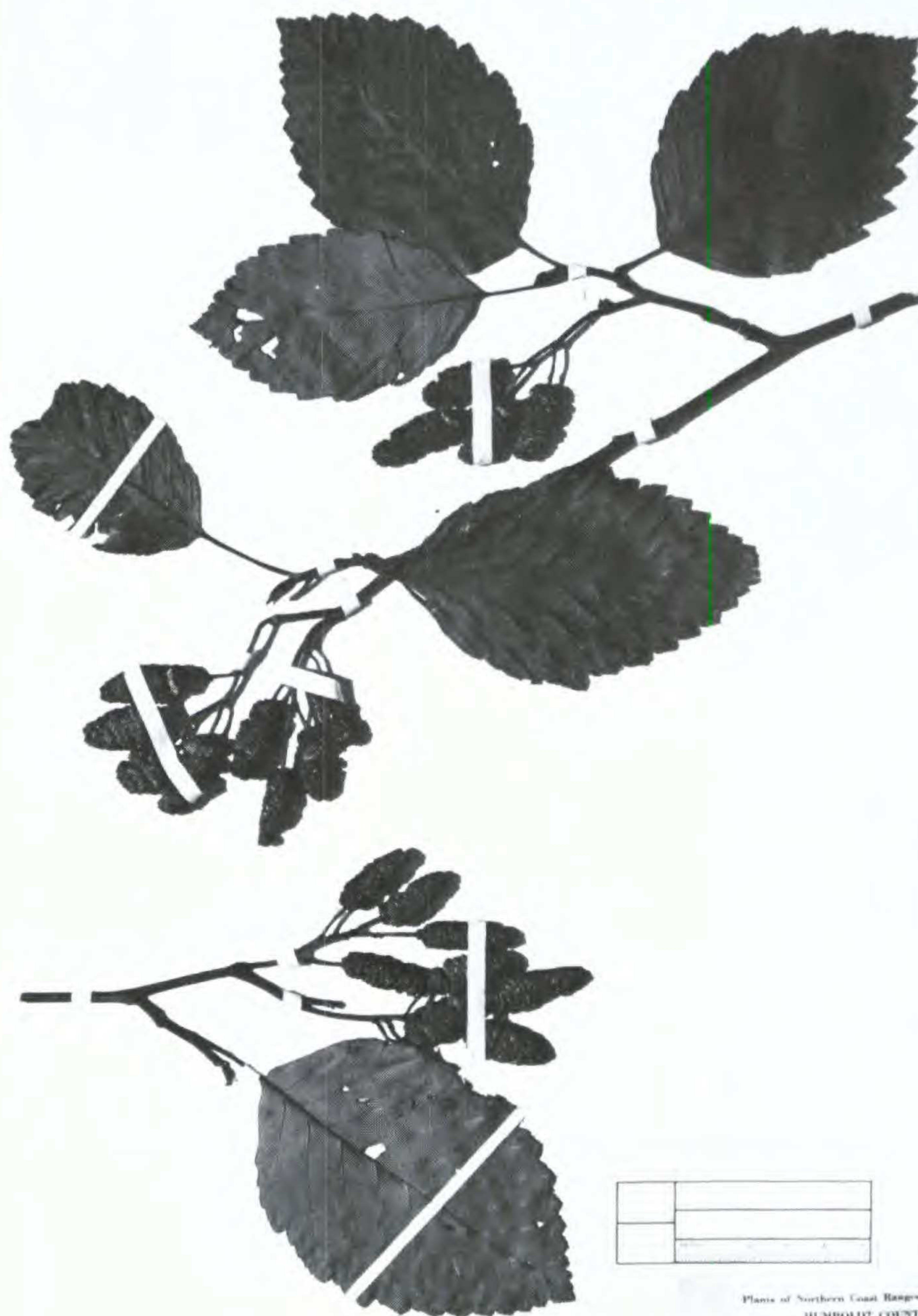
Alnus maritima hort. ex Wetzel, Bot. Archiv **25**: 264. 1929, *non* Spach, Ann. Sci. Nat. ser. 2, **15**: 206. 1841, *pro syn.*

Alnus washingtonia hort. ex Wetzel, Bot. Archiv **25**: 264. 1929, *pro syn.*

Alnus rubra var. *pinnatisecta* Starker, Jour. For. **37**: 415. 1939; *Alnus rubra* f. *pinnatisecta* (Starker) Rehder, Bibl. Cult. Trees and Shrubs, p. 104. 1949. TYPE LOCALITY: "T. Norman Nelson farm, 16 miles northwest of Portland, Ore." (original material not seen).

Narrow, somewhat pyramidal-crowned trees, up to 28 m in height; trunks usually several, erect, up to 1.5 m in diameter; bark thin, gray, whitish, or irregularly mottled, smooth to slightly rough with small bumps and irregularities, with inconspicuous lenticels when young, broken into shallow plates on older individuals; young stems medium to dark red-brown, dull to moderately lustrous, not glaucous to slightly glaucous, usually without a heavy resinous coating, not differentiated into noticeable long and short shoots, often with prominent longitudinal ridges originating at the nodes; internodes usually glabrous, moderately glandular, the glands small to medium in size, brown or dark brown; nodes and stems bearing inflorescences densely glandular; lenticels oval to elongate, 0.5–1.2 mm long, 0.3–1.1 mm wide, whitish to yellowish, moderately prominent; leaf scars 1.5–2 mm high, 2–4 mm wide, the bundle scars moderately prominent. Buds ellipsoid, acute to slightly rounded at the apex, heavily resin-coated; stalk 2–8 mm long, 1.2–2.5 mm in diameter, glabrous, densely glandular; body 6–10 mm long, 3–5 mm in diameter; scales 2 (–3), stipular, equal, more or less valvate,

glabrous to moderately pubescent, glandular; pubescence and glands usually obscured by the heavy coat of resin. Leaves ovate to elliptic; apex acute to obtuse; base broadly cuneate to rounded; blade (3.5–) 6–11 (–15) cm long, (2.5–) 3.5–7 (–9.5) cm wide, medium to dark green and dull to moderately lustrous above, light to medium green or green-brown and dull below, coriaceous; margin strongly revolute, double-serrate or crenate; major teeth (3–) 5–15 (–25) mm apart, 2–6 mm deep (up to 35 mm deep in forma *pinnatisecta* (Starker) Rehder), regular; secondary teeth 3–6 per cm, 0.2–1 mm deep, regular; adaxial surface glabrous to sparsely pubescent, sparsely to moderately glandular; abaxial surface and veinlets glabrous to sparsely pubescent, densely to very densely glandular, slightly to moderately resin-coated; major veins and vein axils near the base usually moderately pubescent to tomentose or wooly-pubescent (rarely only sparsely pubescent); pubescence whitish to yellowish; glands small to medium in size, whitish to yellowish (rarely brownish). Lateral veins 9–14, 4–11 mm apart at mid-leaf, straight or slightly ascending, usually not branching again, terminating in major teeth at the margin; cross veins between lateral veins poorly to well developed. Petioles (7–) 8–18 (–22) mm long, 0.7–2 mm in diameter, sparsely pubescent to moderately villous, moderately to densely glandular. Stipules ovate, elliptic, or obovate, the apex acuminate, acute, or obtuse, 6–8 mm long, 1.7–2.5 mm wide, green to light brown, glabrous to sparsely pubescent, moderately glandular; hairs, when present, yellowish; glands yellowish. Pistillate inflorescences borne in racemose groups of (3–) 4–5 (–8) on short branches diverging moderately to strongly from the main axis, produced during the previous growing season, erect, ovate to elliptic, at anthesis (3.5–) 5–7 mm long, 1.7–2.1 mm in diameter, on peduncles 1–2 mm long, 0.5–1.5 mm in diameter; staminate catkins borne in one or more racemose clusters of (2–) 3–6 at the end of the main branch above the pistillate inflorescences, produced during the previous growing season, pendent during dormancy and anthesis, at anthesis 3.5–14 cm long, 6–10 mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 mm wide. Staminate flowers 3 per bract; perianth of 4 parts, these elliptic to obovate, obtuse to rounded at the apex, 1.6–2.1 mm long, 1.2–1.6 mm wide, lined with minute glands at the margin; stamens 4, opposite and separate from or only slightly basally adnate to the perianth parts, usually appearing much longer than the perianth, filaments 0.8–1.6 mm long, anthers 1.3–1.8



Plants of Northern Coast Ranges of California
HUMBOLDT COUNTY

COLLECTED BY JOSEPH P. TRACY, NO. 2175

11. 24. 1913 - 1914

Alnus

Alnus 2175 - 1914

Figure 25. Representative specimen of *Alnus rubra* Bongard.

mm long and 1.3–1.8 mm in diameter, thecae separate for 30–60% of their length. Mature infructescences ovoid (sometimes ellipsoid) or subglobose, (10–) 14–25 (–34) mm long, (6–) 8–14 (–16) mm in diameter, on peduncles 0.5–7 (–10) mm long, 1–1.8 mm in diameter; scales 4–7 mm long, 4.5–6 mm wide at the apex, 1.7–2 mm wide at the base; apex moderately thick to very thick, flat, the terminal lobe truncate, not extended. Fruits narrowly wing-margined, brown; body ovate or elliptic, 2–2.5 mm long, 1–1.5 mm in diameter; wings 2.5–4 mm long, 0.5–1 mm wide, chartaceous; persistent styles 0.5–0.7 mm long. Figures 2B, 8C, 13D, 18B, and 25.

DISTRIBUTION AND HABITAT: Along the Pacific coast from the southwestern corner of Alaska to central California; east along the Columbia River and its tributaries to eastern Washington and western Idaho. On rocky, gravelly, sandy, or humus stream banks and moist floodplains, lake shores, coasts, and open slopes, at elevations mostly below 300 meters (but occasionally occurring as high as 1,000 meters). Often with *Acer*, *Sequoia*, *Pseudotsuga*, *Thuja*, or *Larix*. Figure 26.

COMMON NAMES: Red alder, Oregon alder, alder.

REPRESENTATIVE SPECIMENS: **Canada.** BRITISH COLUMBIA. North Arm of Cowichan Lake, *Allen s.n.*, Aug. 5, 1938 (cut-leafed) (UC); Bull Harbour, Hope Island off N end of Vancouver Island, *Calder & MacKay 31311* (DAO, UC); 21 mi by road W of Terrace along road to Prince Rupert, *Calder et al. 14928* (DAO, NY, UC); about 2.5 mi E of Masset, Graham Island, *Calder et al. 21299* (DAO); just S of Lawnhill on road from Tiell to Skidegate, Graham Island, *Calder et al. 21737* (DAO); Bowen Island, ca. 5 mi W of Horseshoe Bay, *Huber 1025* (UC); Elk Lake near Victoria, *Macoun s.n.*, Mar. 9, 1914 (CAN); Cowichan Station near Duncan, Vancouver Island, *Wessel 59* (DAO); Prospect Lake near Victoria, *Young 17* (DAO). **United States.** ALASKA. Juneau, *Anderson 6230* (CAN, DAO, F, NY, RM); 13 mi NW of Juneau on Glacier Highway, *Argus & Chunys 6101* (CAN); Washington Bay, Kuiu Island, *Eyerdam 5345* (WTU); on the banks of Indian River in Sitka National Monument, just E. of Sitka, *Heller 14932* (UC, WTU). CALIFORNIA. Alameda Co.: Berkeley, *Bioletti s.n.*, Apr., 1894 (UC); Berkeley, *Blasdale s.n.*, Mar. 12, 1896 (RM). Del Norte Co.: Crescent City, *Applegate 5294* (F, UC). Humboldt Co.: 3 mi NW of Neafus Peak, *Nelson 154* (UC); Trinidad, *Reed s.n.*, July 26, 1941 (DAO); near Carlotta, on Van Duzen River, *Tracy 6149* (UC). Marin Co.: W side of Mount Tamalpais, *Lawfer 131* (WTU). San Mateo Co.: Tunitas, *Rose 36743* (US); Tunitas, *Rose 55189* (RM). IDAHO. Bonner Co.: Whiskey Rock Bay, Pend Oreille Lake, *Johnson 4781* (RM, UC). OREGON. Clatsop Co.: Seaside, *Demaree 13441* (NY). Hood River Co.: without location, *Henderson 312* (MO). Lane Co.: 8 mi SW of Cottage Grove, *Furlow 299* (MSC). Washington Co.: Portland, *Lunnell s.n.*, June 20, 1903 (RM); T. Norman Nelson farm, Dixie Mountain, *Matthews s.n.*, Oct. 3,

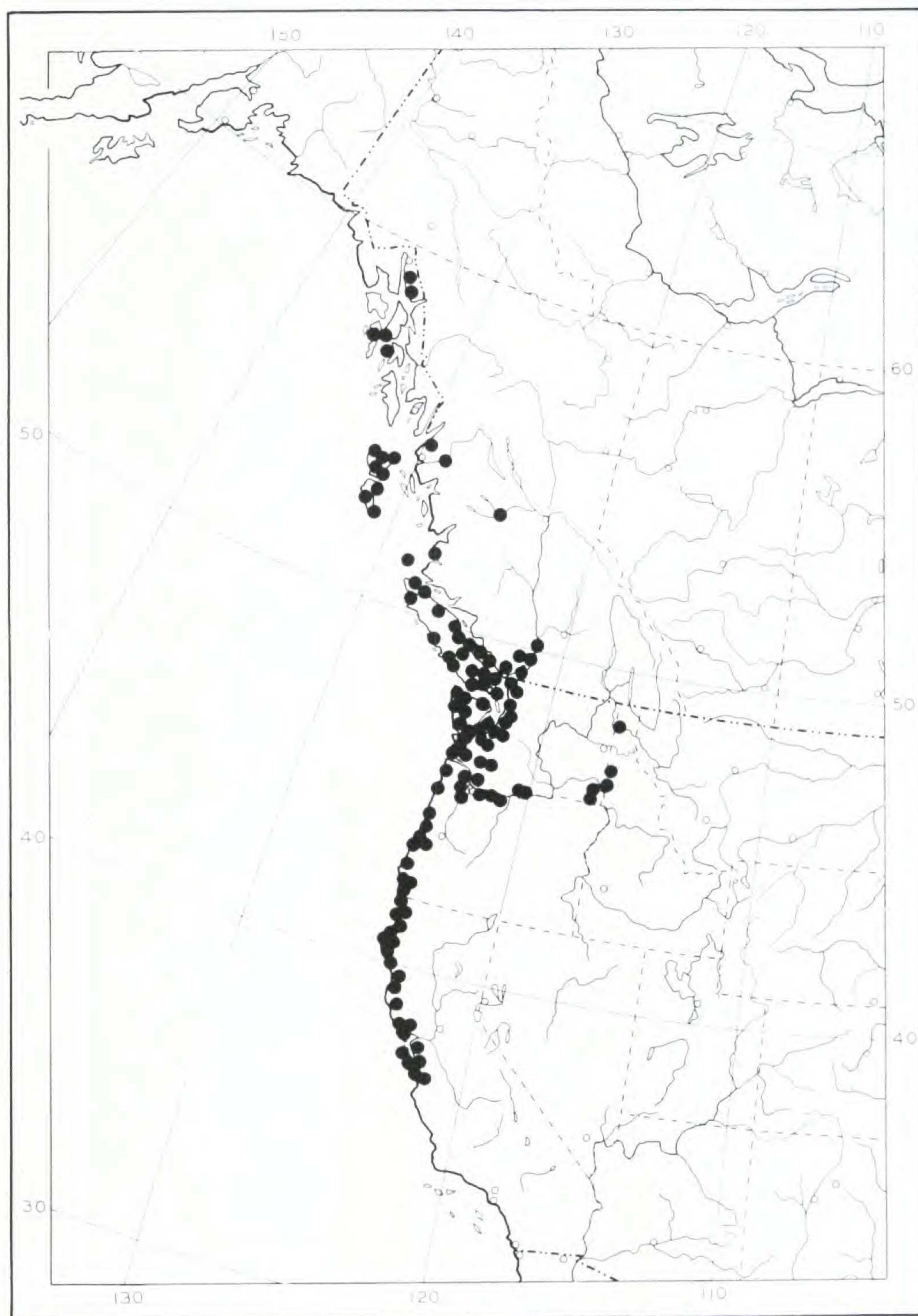


Figure 26. Distribution of *Alnus rubra* Bongard.

1940 (cut-leafed) (UC). WASHINGTON. Clark Co.: Vancouver Lake, *Sheldon 11680* (UC). Grays Harbor Co.: 5 mi SE of Humptulips, *Furlow 293* (MSC). King Co.: Seattle, *Eyerdam 1329* (F, MO); North Seattle, *Eyerdam s.n.*, Aug. 29, 1936 (F, UC); near Seattle, *Thompson 5128* (WTU). Pierce Co.: along the White River 6 mi NW of Cayuse Pass, Mount Rainier National Park, *Furlow 290* (MSC); 7 mi SE of Enumclaw, *Furlow 292* (MSC). Skeminana Co.: E bank of Clearwater Creek, Columbia National Forest, *Matthews s.n.*, Sept. 9, 1940 (cut-leafed) (UC).

Morphologically, *Alnus rubra* appears to be the most generalized species of the genus in America. It is little specialized in terms of habit, leaf shape, leaf size, cone size, and many other features, although it appears to be more or less advanced in a few other characters (including the reduced wings of the fruits).

Nuttall (1842), and later Kuntze (1891), recognized strong affinities between *Alnus rubra* and the alders of Latin America, though this relationship has not frequently been discussed by other authors. Numerical results from the present study, based on both morphological and chemical data, support such a link. *Alnus rubra*, together with *A. acuminata*, *A. jorullensis*, and *A. oblongifolia*, apparently represents a remnant of an ancient complex of species in the New World. Their relationship to the Eurasian species is thus far not well understood, however.

In the western United States and Canada this species was formerly widely known as *Alnus oregona* Nuttall, and this name continues to find limited use today. The name *Alnus rubra* Tuckerman, based on *Betula-alnus rubra* Marshall, is a later homonym applying to *A. serrulata* (Aiton) Willdenow.

Alnus rubra is readily recognized by its large size, gray mottled bark, and ovate, coarsely-toothed, revolute-margined leaves. The largest reported individual occurs in Polk Co., Washington, and has a trunk circumference of 4.1 m, a height of 27.6 m, and a spread of 16.2 m (Pomeroy & Dixon, 1966). In two or three widely-separated locations a form with deeply-cut leaves (*Alnus rubra* f. *pinnatisecta* (Starker) Rehder) occurs sporadically, growing along with individuals of the ordinary kind. The depth of the leaf lobes in such plants is not the same in specimens from various trees or locations.

Alnus rubra is found in varying habitats, ranging from exposed coastal bluffs to river floodplains and pond shores, sometimes forming great expanses of forest in low-lying areas of Washington and Oregon. Mainly restricted to the mesic coastal fog belt, it follows the Columbia River system eastward away from the Pacific

Ocean, reaching western Idaho in several disjunct populations (Johnson, 1968a & b). The limiting factors responsible for the restricted distribution of this species are not well understood. Although it occurs in a rather moderate climate naturally, plants transferred to an experimental garden in central Michigan, where the winters are relatively severe, were found to be perfectly hardy.

2. *Alnus oblongifolia* Torrey

Alnus oblongifolius Torrey in Emory, Rept. U.S. Mex. Bound. Surv. 2: 204. 1859; *Alnus serrulata* γ *oblongifolia* (Torrey) Regel, Bull. Soc. Nat. Mosc. 38(3): 432. 1865. TYPE: Wright 1864, "banks of the Mimbres and near Santa Barbara, New Mexico" (Holotype, NY!; Isotype, US!). Figure 27.

Open, round-crowned trees up to 15 (–30) m in height; trunks usually several, erect, up to 1.5 m in diameter; bark light gray to brown and smooth when young, dark brown and broken into plates on old individuals, the lenticels usually inconspicuous on smooth trunks and branches; young stems medium red-brown, slightly to moderately lustrous, slightly to moderately resin-coated, not differentiated into long and short shoots, sometimes with slightly to moderately conspicuous longitudinal ridges originating at the nodes; internodes sparsely pubescent to velutinous, sparsely to moderately glandular; nodes and stems bearing inflorescences very densely glandular; hairs yellowish to brownish; glands small to medium in size, yellowish to brownish; lenticels of twigs circular to elliptic, 0.2–0.7 mm long, 0.1–0.5 mm wide, whitish, inconspicuous. Buds ovoid, slightly rounded at the apex, moderately to heavily resin-coated; stalk 1.5–4 mm long, 1–1.5 mm in diameter, glabrous to sparsely pubescent, densely glandular; body 4–8 mm long, 1.5–4 mm in diameter; scales 2, stipular, equal, valvate or often incompletely covering the underlying unexpanded leaves, glabrous to moderately villous, glandular; pubescence and glands usually obscured by the resinous coat. Leaves narrowly ovate or lanceolate to elliptic (or occasionally rhombic); apex long to short acuminate or acute (rarely obtuse or rounded); base narrowly to broadly cuneate or rounded; blade (3–) 5–9 (–11) cm long, (2–) 3–6 (–7) cm wide, medium to dark green and dull (sometimes lustrous when young) above, medium green and dull to moderately lustrous below, chartaceous to moderately coriaceous; margin flat, slightly thickened, sharply to coarsely double-serrate to serrulate; major teeth



Figure 27. Right: holotype of *Alnus oblongifolia* Torrey. Left: specimen of *A. acuminata* Humboldt, Bonpland, & Kunth.

usually acuminate, standing well above the secondary teeth, 5–13 (–16) mm apart at mid-leaf, up to 5 mm deep, regular to irregular; secondary teeth 3–8 per cm, 0.5–2 mm deep, slightly uneven to irregular; adaxial surface sparsely pubescent to (rarely) moderately villous (sometimes glabrous), moderately to densely glandular; abaxial surface and veinlets sparsely to moderately villous, moderately to densely glandular, slightly to moderately resin-coated; major veins and vein axils near the base densely tomentose to wooly-pubescent; pubescence whitish to yellowish; glands small to medium in size, whitish to yellowish (rarely brownish). Lateral veins 9–13 (–15), 3–8 mm apart at mid-leaf, straight or slightly ascending, often branching once again, especially near the base, terminating in major teeth at the margin; cross veins between lateral veins poorly developed and usually not meeting. Petioles (3–) 7–18 (–22) mm long, (0.7–) 1–1.5 mm in diameter, moderately villous to velutinous, moderately to densely glandular. Stipules ovate to elliptic or obovate, acute to obtuse at the apex, 5–7 mm long, 1–1.5 mm wide, green to light brown, glabrous to velutinous, the hairs yellowish, moderately glandular, the glands yellow or pale brown. Pistillate inflorescences borne in racemose groups of (2–) 4–5 (–7) on short branchlets not diverging strongly from the main axis, these sometimes subtended by leaves, several such groups also often clustered together, produced during the previous growing season, erect, ovate to elliptic, at anthesis 4–5 mm long, 2–2.8 mm in diameter, on peduncles 1.5–5 mm long, 1–5 mm in diameter; staminate catkins borne in one or more racemose clusters of 3–6 at the summit of the main branch above the pistillate inflorescences, produced during the previous growing season, pendent during dormancy and anthesis, at anthesis 3.2–8.5 (–10) mm long, 5–8 mm in diameter, on peduncles 3–13 mm long, 1–1.5 mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 (–4) mm wide. Staminate flowers usually 3 per bract; perianth of 4 parts, these elliptical to obovate, rounded at the apex, 1.3–1.8 mm long, 0.8–1.2 mm wide, 2 frequently reduced in size, the margins lined with minute glands or glands absent; stamens 2 or 4, if 4 then 2 frequently reduced in size, opposite and basally adnate to the perianth parts, usually appearing much longer than the perianth, the filaments 1–1.3 mm long, the anthers 0.9–1.6 mm long, 1–1.4 mm in diameter, the thecae separate for 50–70% of their length. Infructescences ovoid, ellipsoid, or cylindric, (9–) 15–24 mm long, 0.5–1.5 mm in diameter; scales 3–4 mm long, 2.5–4 mm wide at

the apex, 0.5–1.3 mm wide at the base, the apex thin to moderately thickened, flat, the terminal lobe-tip acute, somewhat to very extended. Fruits narrowly winged, brown; body broadly elliptic to obovate, 1.8–3 mm long, 1.2–2.3 mm in diameter; wings 2.2–3.5 mm long, 0.5–1 mm wide, chartaceous; persistent styles 0.6–1 mm long. Figures 3A, 4A, 8A, 15C, 22B, and 27.

DISTRIBUTION AND HABITAT: Central Arizona and west-central New Mexico south to south-central Chihuahua and northeastern Sonora. Occurring on sandy or rocky streambanks and adjacent moist slopes, often in mountain canyons, from elevations of about 1,500 to 2,300 meters (occasionally as low as 1,000 meters). Often associated with *Pinus*, *Quercus*, *Juniperus*, or *Pseudotsuga*, sometimes fairly dense groves. Figure 28.

COMMON NAMES: Arizona alder, New Mexican alder, Mexican alder, aliso.

REPRESENTATIVE SPECIMENS: **Mexico:** CHIHUAHUA. Cuiteco, S of Creel near Río Cuiteco, *Knobloch* 948 (MSC); Batopilas River, *LeSueur* 1304 (ARIZ, F). Sonora. Huchuerachi, *Hartman* 322 (F, NY, UC, US); 6 mi N of Huachinera, *Hastings & Turner* 65–53 (ARIZ); Cañon Palpito, Mun. de Agua Prieta, *Muller* 3728 (MICH); Cañon de Bavispe, *White* 3116 (MEXU, MICH); Cañon Internacional, *White* 3481 (F, MICH). **United States.** ARIZONA. Apache Co.: Bog Creek, 10 mi E of McNary, *Goddard* 687 (UC). Gila Co.: bank of East Verde River, at bridge N of Payson, *Foster & Arnold* 108 (US); Sierra Ancha, *Jackson* 13 (US); without definite location, *Johnson* 8581 (NY, UC, US). Graham Co.: Mt. Graham, near Wet Canyon Recreation Area, *Furlow* 351 (MSC); Graham Mountains, *Thornber & Shreve* 7849 (ARIZ); Graham Mountains, *Thornber & Shreve* 8011 (ARIZ). Greenlee Co.: Clifton, A.T., *Rusby* 383 (F, NY, UC). Pima Co.: Mt. Lemmon, *Loomis et al.* 2180 (ARIZ). Beaver Creek, *Fernow s.n.*, Aug., 1896 (US). Oak Creek, *Pearson* 338 (US). NEW MEXICO. Grant Co.: Pinos Altos Mts., *Greene s.n.*, Oct. 11 (F). Luna Co.: banks of the Mimbres and near Santa Barbara, *Bigelow s.n.*, without date (NY); without location, *Wright* 1864 (NY, US). Socorro Co.: in the Mogollon Mountains in or near the W fork of the Gila River, *Metcalf* 365 (ARIZ, MO, NY, RM, UC); near Halt's Ranch, in the Mogollon Mountains, *Wootton s.n.*, July 20, 1900 (ARIZ, RM). Pecos Cañon, *Eastwood* 15503 (NY).

Alnus oblongifolia possesses a quite restricted distribution relative to the other North American species of the genus. In Sonora this species intergrades with *A. acuminata* ssp. *arguta*, and a case might be made to combine it with that taxon. Sargent, in *The Silva of North America* (1896), tentatively included it in *Alnus acuminata* pending the accumulation of additional specimens, noting that it appeared to be identical with certain of the Mexican material. In

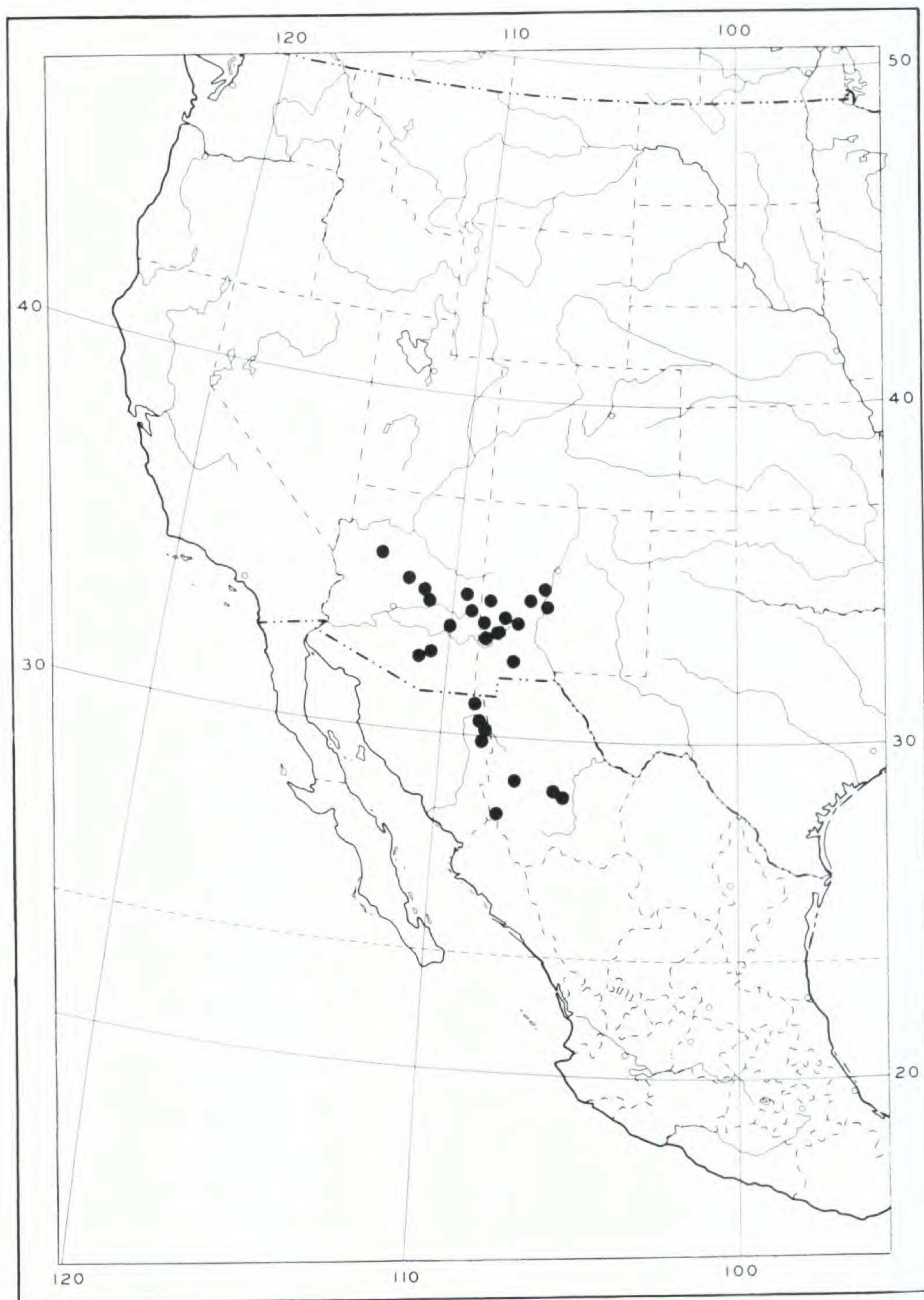


Figure 28. Distribution of *Alnus oblongifolia* Torrey.

many ways, however, *A. oblongifolia* shows affinities to *A. rhombifolia*, with which it is sometimes confused. Characters in *A. oblongifolia* suggesting this relationship include the presence of only two stamens, a tendency to take on a serrulate and rhombic leaf form, and the smooth bark (lacking the transverse constrictions of *A. acuminata*). Its leaf shape varies, often on the same branch, from a distinctive sharp-toothed, lanceolate, acuminate-tipped form to one which is more or less elliptical or rhombic with very small teeth, reminiscent of *Alnus rhombifolia*, to a double-serrate ovate type similar to that of *A. incana* ssp. *tenuifolia* (which occurs in the same geographical region, though at a higher elevation). Identification is usually difficult, however, only with herbarium specimens having few leaves.

Alnus oblongifolia is found at relatively high elevations in the mountains of the southwestern United States and adjacent northern Mexico. The habitat of this species in Arizona is described in detail by Whittaker and Niering (1965) in their study of the vegetation of the Santa Catalina Mountains.

Alnus oblongifolia, like *A. rubra*, is unspecialized in morphology and similarly occupies a mesophytic habitat. Both taxa are probably remnants of wider-ranging species which existed during cooler periods.

3. *Alnus rhombifolia* Nuttall

Alnus rhombifolia Nuttall, North Amer. Sylva **1**: 49. 1842; *Alnus rhombifolia* var. *typica* Callier, Fedde Rep. Sp. Nov. **10**: 229. 1911. TYPE: Nuttall s.n., "in the vicinity of Monterey in Upper California" (BM?, not seen).

Alnus glutinosa δ *serrulata* (Aiton) Regel, Mem. Soc. Nat. Mosc. **13**(2): 166. 1861, in part.

Alnus glutinosa δ *serrulata* lusus d. *californica* Regel, Mem. Soc. Nat. Mosc. **13**(2): 166. 1861. TYPE LOCALITY: "aus Californien" (original material not seen).

Alnus rhombifolia var. *ovalis* Winkler, Pflanzenreich **19**(4.61): 115. 1904. TYPE LOCALITY: "Californien" (original material not seen).

Alnus californica hort. ex Winkler, Pflanzenreich **19**(4.61): 115. 1904, *pro syn.*

Alnus rhombifolia var. *bernardina* Munz & Johnston, Bull. Torr. Bot. Cl. **52**: 222. 1925. TYPE: Munz & Johnston 8468, junction of South Fork and Santa Ana River, San Bernardino Mts., San Bernardino Co., California (Holotype, POM; Isotypes, FI, NY!). Figure 29.

Somewhat pyramidal open-crowned trees up to 25 (–28) m in height; trunks usually several, erect, up to 1 m in diameter; bark light gray, whitish, or irregularly mottled, smooth to slightly rough, with inconspicuous lenticels when young, brown and broken into scales on old individuals; young stems light green to red-brown, slightly to moderately lustrous, slightly to moderately glaucous, lightly to moderately resin-coated, not differentiated into long and short shoots, usually without longitudinal ridges; internodes glabrous to moderately villous, sparsely to moderately glandular; nodes and stems bearing inflorescences very densely glandular; hairs whitish to yellowish; glands small, yellowish to brownish; lenticels of twigs circular to elliptic, 0.1–0.7 mm long, 0.1–0.3 mm wide, whitish, inconspicuous; leaf scars 1.7–2 mm high, 1.5–2.5 mm wide, the bundle scars moderately prominent. Buds ellipsoid to obovoid, slightly rounded at the apex, moderately to heavily resin-coated; stalk 3–5 mm long, 1.2–1.5 mm in diameter, glabrous to sparsely pubescent, moderately to densely glandular; body 3–9 mm long, 2–3 mm in diameter; scales 2, stipular, equal, mostly valvate, often incompletely covering the underlying organs or even apparently absent from the buds nearest the apex of the stem, glabrous to moderately villous, glandular; pubescence and glands often obscured by the heavy resin coat. Leaves ovate, elliptic, or rhombic; apex acute, obtuse, or rounded (rarely acuminate); base broadly cuneate to rounded; blade (3–) 4.5–8.5 (–13) cm long, (1.5–) 2.5–4.5 (–7.5) cm wide, medium to dark green and dull (sometimes lustrous when young) above, light to medium green and dull to moderately lustrous below, chartaceous to coriaceous; margin flat, not thickened, finely serrate, serrulate, or (rarely) double-serrate (mainly on very vigorous shoots), sometimes slightly lobed; major teeth 5–8 (–10) mm apart at mid-leaf, up to 3 mm deep, regular to irregular; secondary teeth 4–9 per cm at mid-leaf, 0.7–1.5 mm deep, slightly uneven to irregular; adaxial surface glabrous, sparsely pubescent, or moderately villous, moderately to densely glandular; abaxial surface and veinlets sparsely pubescent to velutinous, moderately to densely glandular, slightly to moderately resin-coated; major veins and vein axils near the base densely tomentose to wooly-pubescent; pubescence whitish to yellowish; glands small to medium in size, yellowish to brownish. Lateral veins 9–12 (–15), (2–) 4–7 (–10) mm apart at mid-leaf, straight, often branching once again, especially near the base, terminating in major teeth at the margin; cross veins between



Figure 29. Specimen of *Alnus rhombifolia* Nuttall. Isotype of *Alnus rhombifolia* var. *barnardina* Munz & Johnston.

lateral veins usually poorly developed. Petioles (3-) 7-15 (-23) mm long, 0.7-1.2 (-1.8) mm in diameter, moderately villous to velutinous, moderately to densely glandular. Stipules mostly elliptic, the apex acute, 6-11 mm long, 2-2.5 mm wide, green to light brown, glabrous to moderately villous, the hairs yellowish, moderately glandular, the glands yellowish. Pistillate inflorescences borne in racemose groups of 3-6 on short non-strongly-divergent branchlets, produced during the previous growing season, erect, ovate to elliptic, at anthesis 3-6 mm long, 1.5-2 mm in diameter, on peduncles 0.5-1.5 mm long, 0.6-1 mm in diameter; staminate catkins borne in one or more racemose clusters of 3-7 at the end of the main branch above the pistillate inflorescences, produced during the previous growing season, pendent during dormancy and anthesis, at anthesis 3-10 cm long, 4-7 mm in diameter, on peduncles 2-12 mm long, 1-1.5 mm in diameter; floral bracts 1-2 (-3) mm high, (1.5-) 2-3 (-3.5) mm wide. Staminate flowers 3 per bract; perianth of 4 parts, these elliptic or obovate, the apex obtuse to rounded, 0.9-1.7 mm long, 0.4-1.1 mm wide, 2 frequently reduced, the margin lined with minute glands or glands absent; stamens usually 2 (occasionally 4, but if so 2 reduced), opposite and basally adnate to the perianth parts, usually appearing much longer than the perianth; filaments 0.8-1.7 mm long, anthers 1.1-1.9 mm long and 1.2-1.7 mm in diameter, the thecae separate for 35-45% of their length. Infructescences ovoid, ellipsoid, or cylindrical, 10-17 (-22) mm long, (6-) 7-9 (-10) mm in diameter, on peduncles 0.2-7 (-10) mm long, 0.7-1.2 mm in diameter; scales 3-3.5 mm long, 3.5-4.2 mm wide at the apex, 1-1.2 mm wide at the base, the apex moderately thickened, flat, the terminal lobe-tip acute to rounded and somewhat extended. Fruits narrowly wing-margined, brown; body broadly elliptic, 2-2.5 mm long, 1.5-2 mm in diameter; wing margins 2.5-3 mm long, 0.1-0.3 mm wide; persistent styles 1-1.5 mm long. Figures 3C, 7C, 9C, 18A, 29, and 30.

DISTRIBUTION AND HABITAT: Southern Washington and adjacent western Idaho southwest to northern California and south to the Mexican border. On rocky streambanks and adjacent slopes from near sea level at the coast to elevations of over 2,300 meters inland. Often associated with *Pinus*, *Quercus*, or *Abies*. Figure 31.



Figure 30. Representative specimen of *Alnus rhombifolia* Nuttall.

COMMON NAMES: Alder, white alder, California alder, mountain alder, western alder.

REPRESENTATIVE SPECIMENS: **United States.** CALIFORNIA. Alameda Co.: along Redwood Creek, NE of Redwood Peak, *Constance* 380 (UC). Contra Costa Co.: Alamo Canyon, Mount Diablo, *Bowerman* 1058 (UC). Del Norte Co.: Kelley's Flat, Darlingtonia, Smith River, *Parks & Parks* 24084 (RM). Humboldt Co.: along the Trinity River 7 mi SE of Willow Creek, *Furrow* 304 (MSC). Los Angeles Co.: San Antonio Cañon near Claremont, *Baker* 3667 (F, MO, NY, RM, US); Little Dalton Canyon, San Gabriel Mts., *Campbell* 82 (DAO). Mariposa Co.: along the Merced River, 5 mi W of Yosemite Village, Yosemite National Park, *Furrow* 307 (MSC). Mendocino Co.: by streams, Ukiah, *Pringle s.n.*, Aug. 14, 1902 (F); 12 mi N of Leggett along US 101, along S fork of Eel River, *Stevens* 1072 (MSC). Nevada Co.: W of Greenhorn Creek, T16N, R9E, S24, *Raven* 8014 (F). Riverside Co.: along stream, Snow Creek, N base of San Jacinto Mts., *Roos* 2403 (WTU); Whitewater, *Rose* 38003 (NY, WTU). San Bernardino Co.: junction of South Fork and Santa Ana Rivers, San Bernardino Mts., *Munz & Johnston* 8468 (F, WTU); mouth of Mill Creek, *Munz & Johnston* 8679 (NY); San Bernardino Valley, *Parish & Parish* 542 (F, JEPS, UC). San Diego Co.: on bank of San Felipe Creek above ranch house of San Felipe Ranch, *Wiggins* 2031 (WTU). Siskiyou Co.: Shasta River, *Butler* 10 (UC). Tehama Co.: Cold Fork of the Cottonwood Creek, near foot of Tom's Head, Yollo Bolly Mtns., *Jepson s.n.*, Apr. 28, 1899 (JEPS). Trinity Co.: along the Trinity River 5 mi NW of Del Loma, *Furrow* 305 (MSC). Ventura Co.: 1¼ mi NW of Casitas, *Sowder* 145 (UC); Horn Cañon, Ojai, *Thacher s.n.*, Apr. 24, 1918 (JEPS). IDAHO. Canyon Co.: Big Willow, *Macbride* 128 (RM). Clearwater Co.: Orofino, *Christ* 7511 (NY). Latah Co.: near Kendrick, *Christ* 10151 (NY). Nez Perces Co.: about Lewiston, *Heller & Heller* 3117 (DAO, MO, NY, UC). OREGON. Hood River Co.: E line of county, *Henderson* 813 (MO). Jackson Co.: Neil Creek, 6 mi S of Artland, *Applegate* 960 (UC); Gold Hill, *Walpone* 150 (US). Malheur Co.: upper end of Sucker Creek Canyon, 25 mi S of Adrian, *Clarkson* 264 (DAO). Wasco Co.: along the Deschutes River, *Jones* 8582 (WTU). WASHINGTON. Klickitat Co.: along creeks near Bingen, *Suksdorf s.n.*, Feb. 13, Mar. 18, 1893 (UC); streams, W Klickitat Co., *Suksdorf s.n.* Mar. 2, May, 1881 (F, UC). Whitman Co.: along stream on N side of Snake River, 14 mi W of Lewiston, *Hitchcock & Muhlick* 22029 (RM, UC, WTU).

In certain populations *Alnus rhombifolia* has very pubescent leaves. Such a variant was designated var. *bernardina* by Munz and Johnston (1925). However, study of the species in all parts of its range in western North America showed that this form merely represents one extreme in the overall pattern of variation and does not warrant formal recognition.

Occasionally, especially on vigorous sprouts and young plants, the leaves assume a more lanceolate form with the tip becoming acuminate and the margin double-serrate, suggesting somewhat the shape of *Alnus oblongifolia*, to which it is closely allied. The largest

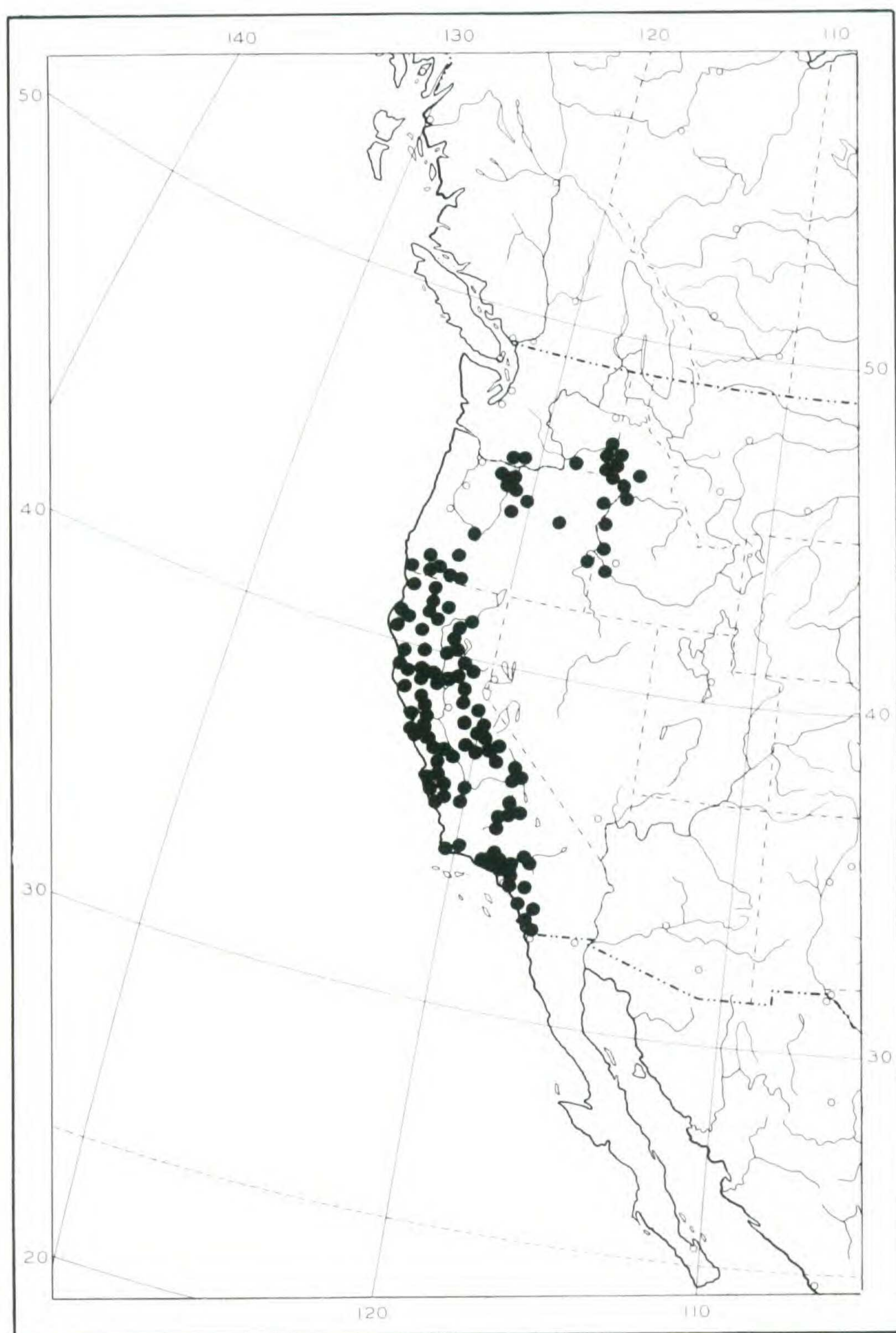


Figure 31. Distribution of *Alnus rhombifolia* Nuttall.

known individual, as reported by Dixon (1961), occurs in the Angeles National Forest in California, measuring 28.4 meters in height, 13.7 meters in spread, and 3.4 meters in trunk circumference.

This alder often occurs in habitats with moderately warm winters; in the southern part of its range it retains its leaves most of the year, though in the North it is deciduous during the winter. It survives, as well, in some more rigorous situations (e.g., in the Sierra Nevada Mountains). Young plants from Shasta Co., California (collected at an elevation of about 20 meters above sea level), when transplanted to an experimental field at Lansing, Michigan, were killed back to ground level during each of four consecutive winters, but they always resumed vigorous growth the following spring.

Specimens from northern Mexico were not seen, but since *Alnus rhombifolia* is known to occur as far south as San Diego, California, populations might be expected to exist in adjacent Baja California as well.

4. *Alnus acuminata* Humboldt, Bonpland, & Kunth

Alnus acuminata Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. Pl. 2: 20. 1817.

Narrow-crowned trees up to 30 m in height; trunks one or several, erect to spreading, up to 1 m in diameter; bark gray to gray-brown, smooth to slightly rough, scaly on old individuals, often broken by transverse ridges or constrictions encircling the stem; young stems medium green-brown, brown, or dark red-brown, dull to moderately lustrous, sometimes slightly to heavily glaucous, without conspicuous longitudinal ridges originating at the nodes; internodes glabrous to moderately villous or velutinous, moderately to densely glandular; nodes and stems bearing inflorescences densely glandular; hairs yellowish to brown (occasionally dark brown); glands small to medium in size, yellowish, brownish, or dark brown; lenticels of twigs circular to elliptic or elongate, 0.3–1.5 mm long, 0.2–1 mm wide, whitish or yellowish, inconspicuous to moderately prominent; leaf scars 1–3 mm high, 1.5–4 mm wide, with inconspicuous bundle scars. Buds ovoid, ellipsoid, or obovoid, acuminate or acute (to slightly rounded) at the apex, lightly to heavily resin-coated; stalk 1–7 mm long, 1–2 mm in diameter, glabrous to moderately villous or velutinous, densely glandular; body 3–10 mm long, 2–4.5 mm in diameter; scales 2, more or less equal, stipular, valvate, often incompletely covering the underlying organs, gla-

brous to sparsely pubescent (to rarely densely villous), glandular; pubescence and glands usually obscured by the resinous coating. Leaves lanceolate, narrowly to broadly ovate, oblong-ovate, elliptic, or (infrequently) obovate; apex long-acuminate, acuminate, acute, obtuse, or rounded; base acute, cuneate, obtuse, or rounded, sometimes oblique; blade (3.5-) 5.5-14 (-19) cm long, (2-) 3-9 (-10.5) cm wide, medium to very dark green and dull, moderately lustrous, or very lustrous above, light to medium green or brown and dull below, chartaceous to coriaceous; margin slightly to moderately revolute or sometimes nearly flat, unthickened or slightly thicker than the blade itself, coarsely, moderately, or finely double-serrate to serrulate; major teeth 8-14 (-20) mm apart, up to 5 mm deep, regular, slightly uneven, or irregular; secondary teeth (2-) 4-8 (-10) per cm, (0.1-) 0.3-1.5 mm deep, regular, slightly uneven, or irregular; adaxial surface glabrous to sparsely pubescent (rarely moderately villous), sparsely to densely glandular; abaxial surface and veinlets glabrous to moderately villous (sometimes tomentose), densely glandular, moderately resin-coated; major veins and vein axils near the base tomentose to wooly-pubescent; pubescence whitish, yellowish, or brown; glands small to medium in size, whitish, yellowish, or brownish (rarely dark brown). Lateral veins (7-) 10-15 (-18), (3-) 5-8 (-15) mm apart at mid-leaf, straight to slightly ascending, usually branching once again, especially near the base, terminating in major teeth at the margin; cross veins between lateral veins poorly to well-developed. Petioles (4-) 7-23 (-35) mm long, (0.8-) 1-2 (-2.5) mm in diameter, glabrous to velutinous, moderately to densely glandular. Stipules ovate to elliptic, the apex acuminate to acute, 4-8 mm long, 1-1.5 mm wide, green to light brown, sparsely pubescent to velutinous, the hairs yellowish to brownish, moderately glandular, the glands yellowish. Pistillate inflorescences borne in racemose groups of (2-) 3-6 on short non-strongly-divergent to strongly-divergent branchlets, these generally subtended by leaves, produced during the previous growing season, erect, ovate to elliptic, at anthesis 3-6 (-8) mm long, 1.5-2.2 (-3) mm in diameter, on peduncles (1-) 2-5 (-6) mm long, 1-1.5 (-2) mm in diameter; staminate catkins borne in one or more racemose clusters of 2-6 at the end of the main branch above the pistillate inflorescences, the lowermost often subtended by small leaves, produced during the previous season, pendent during and before anthesis, at anthesis (3-) 5-11 (-15) cm long, 5-10 (-11) mm in

diameter, on peduncles 2–10 (–22) mm long, 1–1.8 (–2) mm in diameter; floral bracts 1–2 (–3) mm high, (1.5–) 2–3 (–3.5) mm wide. Staminate flowers 3 per bract; perianth of 4 parts, these elliptic or obovate, the apex rounded to obtuse, 1.2–1.8 mm long, 0.6–1.2 mm wide, the margins lined with small to large glands; stamens 4, opposite and basally adnate to the perianth parts, appearing shorter than to longer than the perianth, the filaments 1.1–1.8 mm long, the anthers 1.2–2 mm long and 0.9–1.9 mm in diameter, the thecae separate for 35–55% of their length. Infructescences ovoid, ellipsoid, or cylindric, 11–28 (–45) mm long, 8–12 (–15) mm in diameter, on peduncles 0.2–10 mm long, 1–2 mm in diameter; scales 3–5 mm long, 2.5–5 mm wide at the apex, 1–1.8 mm wide at the base, the apex moderately thickened and flat, the terminal lobe-tip acute to rounded and not much extended to very extended. Fruits narrowly wing-margined, dark brown; body elliptic, to obovate, 1.5–3 (–5) mm long, 1.5–1.8 (–2) mm in diameter; wings 2–3 (–5.5) mm long, 0.2–1 mm wide, chartaceous to coriaceous; persistent styles 0.5–1 mm long.

The taxonomic status of *Alnus acuminata* and the other species of this genus described by Humboldt, Bonpland, and Kunth, *A. jorullensis* and *A. ferruginea*, has long been confused. Virtually all of the Latin American alders have gone under each of these names in one treatment or another. In his monograph of the Betulaceae, Regel (1861) used the name *A. acuminata* for the South American alders, including *A. jorullensis* of Mexico as a variety. The remaining Mexican forms were separated as *A. arguta* (Schlechtendal) Spach, and the extremely narrow-leafed *A. castaneifolia* Mirbel of South America was left as a separate species. Winkler (1904), in his monograph of the family, transferred all of the forms, including *A. castaneifolia*, to *A. jorullensis*, where they were retained in the most recent treatment of the genus by Murai (1964). These taxa are very closely related, but there are consistent differences, at least between *A. acuminata* and *A. jorullensis*.

Photographs of the types at Paris show that the leaves of *Alnus acuminata* are broadly ovate and acuminate-tipped, while those of *A. jorullensis* are more elliptical or obovate with acute or rounded apices. On the basis of the material examined in this study, *A. jorullensis* does not occur farther south than Guatemala, while *A. acuminata* extends deep into South America.

Alnus ferruginea has frequently been used as the name of an extremely pubescent alder, whether in South America, where it was originally collected, or in Mexico and Central America. This pubescent-leaved form is much more frequent in extreme southern Mexico (Chiapas and Oaxaca), Central America, and northern South America than in other parts of the range of the complex, but it represents no more than an extreme in the continuous variation pattern of the pubescence character in this species.

Alnus acuminata is considerably variable throughout its range, but probably not much more so than such other wide-ranging species of the genus as *A. viridis*, *A. incana*, and *A. glutinosa*. Especially variable characters in *Alnus acuminata* include leaf pubescence (which ranges from almost totally absent in some plants to very dense in others), the density and size of the glands covering the lower leaf surface, leaf shape (varying from narrowly lanceolate to nearly orbicular), and the shapes of the leaf apices and bases. The fact that the foliage is so variable sometimes makes this species confusing and difficult to determine, but taken as a whole, it forms a discrete and natural unit.

The area of best development of *Alnus acuminata*, and also of its greatest variability, is southern Mexico and northern Central America, pointing to this region as a possible site of origin. This species is relatively unspecialized, as discussed above, and it may have been derived from a widespread prototype similar to present day *Alnus rubra*, having a mesophytic habitat and a large stature. *Alnus acuminata* and *A. rubra* are similar in many ways, indicating such a close relationship, but these taxa also possess numerous differences, suggesting a long period of isolation.

4a. *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. **acuminata**

Alnus acuminata Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. Pl. 2: 20. 1817; *Alnus acuminata* α *genuina* Regel, Mem. Soc. Nat. Mosc. 13(2): 147. 1861; *Alnus jorullensis* var. *acuminata* (Humboldt, Bonpland, & Kunth) Kuntze Rev. Gen. Pl. 2: 638. 1891. TYPE: *Humboldt & Bonpland s.n.*, "crescit in Andibus Peruviae inter Caxamarca et Micuicampa, regione Escalloniae et Valleae stipularis alt. 1700-1800 hex." (Holotype, P; microfiche photograph of type, MSC!).

Alnus ferruginea Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. Pl. 2: 21. 1817; *Alnus acuminata* γ *ferruginea* (Humboldt, Bonpland, & Kunth) Regel, Mem. Soc. Nat. Mosc. 13(2): 148. 1861; *Alnus jorullensis* var. *ferruginea* (Humboldt, Bonpland, & Kunth) Kuntze, Rev. Gen. Pl. 2: 638. 1891; *Alnus ferruginea* var. a.



Figure 32. Representative specimen of *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*.

- typica* Callier, Mitt. Deutsch. Dendr. Ges. **27**: 161. 1918, in part. TYPE: Humboldt & Bonpland s.n., "crescit locis excelsis frigidis Andium Novogranatensium prope Santa Fé de Bogota, alt. 1400–1600 hex." (Holotype, P; microfiche photograph of type, MSC!).
- Alnus castaneaefolia* Mirbel, Mem. Mus. Hist. Nat. **14**: 463. 1827; *Alnus jorullensis* β *castanifolia* (Mirbel) Regel, Bull. Soc. Nat. Mosc. **38**(3): 425. 1865. TYPE: Dombey, "à Tarma au Perou" (P?, not seen).
- Alnus mirbelii* Spach, Ann. Sci. Nat. ser. 2, **15**: 204. 1841; *Alnus acuminata* β *mirbelii* (Spach) Regel, Mem. Soc. Nat. Mosc. **13**(2): 148. 1861; *Alnus jorullensis* var. ϵ *mirbelii* (Spach) Winkler, Pflanzenreich **19** (4.61): 126. TYPE LOCALITY: "Peruvia" (original material not seen).
- Alnus arguta* δ *punctata* Regel, Mem. Soc. Nat. Mosc. **13**(2): 152. 1861. TYPE: Ruiz, "in Peru und Chili" (not seen).
- Alnus lindeni* Regel, Mem. Soc. Nat. Mosc. **13**(2): 144. 1861. TYPE: Linden, "auf der Sierra Nevada von Neugranada . . . in einer Höhe von 15000 fuss über dem Meere" (original material not seen).
- Alnus acuminata* γ *spachii* Regel, Bull. Soc. Nat. Mosc. **38**(3): 424. 1865; *Alnus spachii* (Regel) Callier in Schneider, Ill. Handb. Laubh. **1**: 132. 1904, *pro syn.*; *Alnus spachii* (Regel) Callier, Mitt. Deutsch. Dendr. Ges. **27**: 163. 1918. Original material not seen.
- Alnus lanceolata* Philippi, Anal. Univ. Chile **91**: 514. 1895. TYPE: Paulus Ortega s.n., "Januario 1881, prope Lurin haud procul a Lima in regione litorali Peruviae" (not seen).
- Alnus rufescens* Liebman ex Hemsley, Biol. Centr. Amer. Bot. **55**: 165. 1882, in part, *pro syn.*
- Alnus jorullensis* var. ζ *acutissima* Winkler, Pflanzenreich **19**(4.61): 127. 1904; *Alnus acutissima* (Winkler) Callier, Mitt. Deutsch. Dendr. Ges. **27**: 163. 1918; *Alnus mirbelii* var. *acutissima* (Winkler) Callier, Mitt. Deutsch. Dendr. Ges. **27**: 163. 1918, *pro syn.* (erroneously attributed to Winkler). TYPE: Peoppig, "Peru: an Bächen des Huanuca-Thals" (Syntype, B?, not seen); Weberbauer 182, "Thal von Huillapolschi, südwärts von Matucana" (Syntype, B?, not seen).
- Alnus ferruginea* var. *aliso* Lorenz & Hieronymus ex Winkler, Pflanzenreich **19**(4.61): 126. 1904, *pro syn.*
- Alnus ferruginea* var. *obtusifolia* Callier, Mitt. Deutsch. Dendr. Ges. **27**: 162. 1918. TYPE: Hartwig 1319, "Colombia: Bogotá, in Andibus" (BRM?, not seen).

Rather narrow-crowned trees up to 25 m in height, sometimes shrubby, sprawling, or prostrate on exposed sites; trunks one to several, up to 1 m in diameter; young stems dull to moderately lustrous, occasionally slightly to moderately glaucous, the internodes sparsely pubescent to velutinous, the glands small to medium in size, yellowish to brownish. Lenticels of twigs 0.3–1 mm long, 0.2–0.7 mm wide, yellowish, moderately prominent. Buds ovoid to ellipsoid, acuminate to acute at the apex, lightly to moderately resin-coated; stalk 1–5 mm long, moderately villous to velutinous; scales sparsely pubescent to densely villous. Leaf apex long-acumi-

nate to acute, obtuse, or rounded; base cuneate to rounded, sometimes oblique; blade 3.6–9.5 (–19) cm long, (2–) 3.5–9 (–11) cm wide; margin slightly to moderately revolute, the major teeth 8–17 mm apart, slightly uneven to irregular; secondary teeth (2–) 3–7 per cm, 0.1–1.5 mm deep, slightly uneven to irregular; abaxial surface and veinlets sparsely to moderately villous or velutinous. Lateral veins (7–) 10–16 (–18), (3–) 4–8 (–15) mm apart at mid-leaf, slightly to moderately ascending; cross veins between lateral veins well-developed. Petioles (4–) 7–16 (–28) mm long, 1–1.8 (–2.5) mm in diameter, glabrous to moderately villous or velutinous. Stipules 7–15 mm long, 2.5–4 mm wide, moderately villous to velutinous. Pistillate inflorescences at anthesis 3–8 mm long, 1.5–3.2 mm in diameter, on peduncles 1.5–6 mm long, 1–1.8 (–2) mm in diameter. Staminate catkins at anthesis 3.5–15 cm long, 5–11 mm in diameter, on peduncles 4–22 mm long, 1–2 mm in diameter. Staminate flowers with 4 perianth parts, these obtuse to rounded at the apex, 1.2–2.2 mm long, 0.6–2 mm wide, the margins lined with small to medium-sized glands; stamens appearing shorter than, equal to, or longer than the perianth, the filaments 0.8–1.8 mm long, the anthers 1.2–2 mm long and 1.1–1.9 mm in diameter, the thecae separate for 20–50% of their length. Infructescences (11–) 15–30 mm long, 8–12 (–15) mm in diameter, on peduncles 1–8 (–10) mm long, 1.2–2 mm in diameter; scales 3–5 mm long, 2.5–4.5 mm wide at the apex, 1–1.7 mm wide at the base. Fruits narrowly wing-margined; body 2.7–3 (–4) mm long, 1.2–1.8 mm in diameter; wings 2–3 mm long, 0.2–1 mm wide, chartaceous to coriaceous; persistent styles 0.5–1 mm long. Figures 16A, 32, and 33.

DISTRIBUTION AND HABITAT: Eastern Venezuela and northern Colombia south along the Andes to northern Argentina. On streambanks and moist slopes at elevations from 2,000 to 2,800 meters (occasionally extending as low as 1,500 meters). Figure 34.

COMMON NAMES: Aliso, jaul.

REPRESENTATIVE SPECIMENS: **Argentina.** Villa Nougues, Prov. Tucumán, *Krapovickas & Cristobal* 14529 (MO, UC); Saladillo, Prov. Tucumán, *Mayer* 13,956 (MO); de Yala a Lagunas de Yala, Prov. Jujuy, *O'Donnell* 2854 (NY); Cerro la Cuera Sta. Cruz, Prov. Salta, Dept. Orán, *Pierotti* 323 (NY, UC); Sierra del Cajón, Prov. Salta, *Rodrequez* 1291 (NY); Hogava, *Venturi* 1047 (UC); Siacubon, *Venturi* 3865 (MO); la lagunita, Prov. Tucumán, Dept. Tafí, *Xescorle s.n.*, Jan., 1944 (NY, UC). **Bolivia.** La Paz, *Buchtien* 680 (MO, NY); location illegible, *Buchtien* 3146 (NY, US); Tunari, *Kuntze*



Figure 33. Specimen of *Alnus castaneifolia* Mirbel (= *A. acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata*).

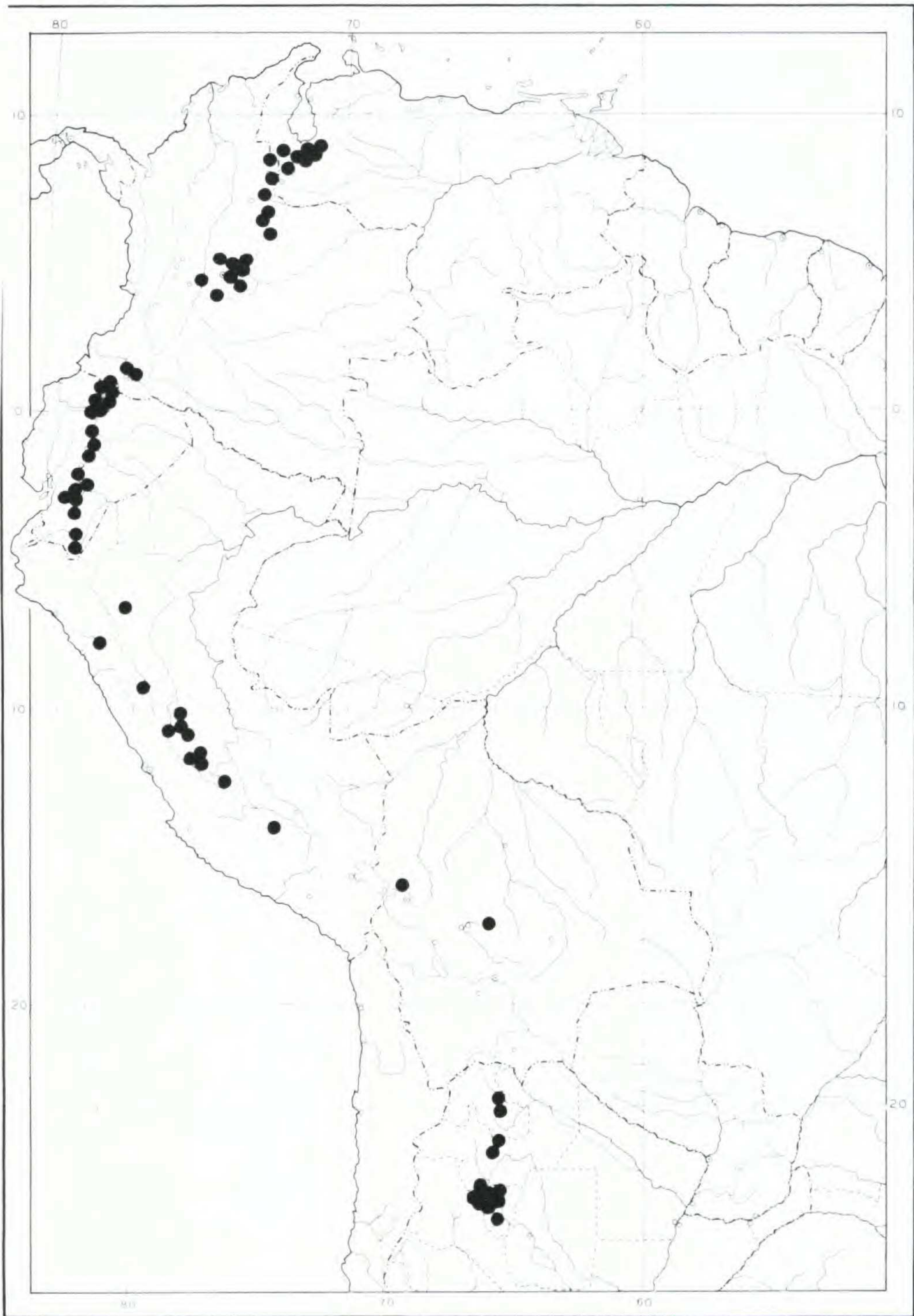


Figure 34. Distribution of *Alnus acuminata* Humboldt, Bonpland, & Kunth ssp. *acuminata* in South America.

s.n., Apr. 5, 1892 (NY, US); Pulcheri *White* 234 (MICH, NY). **Colombia.** Boqueron de Bogotá, *Andre* 720 (NY); Páramo de Guasca, Cundinamarca, *Balls* B5768 (UC); Caldas E of Neira, near Cemento de Caldas, *Breteler* 4472 (NY); Dept. Norte de Santander, E slope of Páramo de Santurbán, toward Mutiscus, *Killip & Smith* 19615 (NY); canoncito in sabrano, Dept. of Cundinamarca SW of Las Cruces, Bogotá, *Pennell* 2131 (NY); Páramo de San Antonio, entre la Laguna de La Cocha y el Valle de Sibundoy, Prov. Putumayo, *Schultes* 3221A (F). **Ecuador.** Chillo Valley, Río Pita, *Anthony & Tate* 229 (US); Prov. Loja, Cerro Villanaco, ca. 7 km W of the city of Loja, *Camp* E-676 (NY); Prov. Azuay, along the Río Cumbe, 25–30 km S of Cuenca, *Camp* E-2070 (F, NY); valley of the Río Matadero, a few km W of Cuenca, *Giler* 37 (US); Provs. Imbabura and Pichincha, Otavato to Maichiugui, *Hitchcock* 20820 (NY); Río Tasquasa near Angel, *Mexia* 7536 (UC); vicinity of Cuenca, *Rose* 22855 (NY); in Andibus Equadorensibus, *Spruce* 5755 (NY); N side of valley of el Río Leon, 85 km S of Cuenca, *Wiggins* 10846 (MO, NY, UC). **Peru.** Valle del Urubamba, Calca, *Herrera* 2092 (F); Canyon of Río Huasahuasi below Huasahuasi, *Hutchinson* 1057 (NY, UC); Tarma, *Macbride & Featherstone* 1021 (F); Cerro Puma Urco, SE of Chachapoyas, *Pennell* 15526 (US); Río Acopalca, *Rauh* *s.n.*, July 3, 1957 (F); in Peruviae memonibus, *Ruiz* 11652 (F, photograph); without location, *Ruiz & Pavon* *s.n.*, in 1788 (F); km 40, Dept. Huanuco, Huanuco to Carpath, *Seibert* 2222 (MO, US); alrededores de Huancayo, *Tovar* 2770 (UC); Cuzco, *Vargas* C. 8109 (MO); Dept. Apurimac, *Vargas* C. 8766 (MO); vicinity of Pano, *Woytkowski* 112 (F). **Venezuela.** Chama valley, Apartaderos, *Breteler* 4475 (NY); Chama valley, between Nuechies and San Rafael, *Breteler* 4480 (NY); Valle Río Chama, 9 km from Mérida along road to Tabay, *Breteler* 4481 (NY); Quebrada de Saisay, *Gehriger* 24 (NY); Mérida, *Jahn* 788 (NY); Moconoque, Mer., everywhere, *Pittier* 13239 (MO, NY).

Alnus acuminata ssp. *acuminata* is the only alder occurring in South America. Several minor variants, including *A. mirbelii* Spach, *A. spachii* Callier, and *A. acutissima* Callier, differ only in leaf margin and indumentum, and in these characters not consistently; therefore these taxa are not recognized as distinct. Regionally, *Alnus acuminata* ssp. *acuminata* has generally smaller leaves and infructescences toward the southern part of its range (Argentina) than it does in the center (Bolivia and Peru). Farther north, in populations in Venezuela, Colombia, and Ecuador, the leaves are broader and more rounded at the apex, although acuminate-tipped foliage is not entirely absent, while the infructescences are somewhat smaller than those from populations in the central part of the range.

The foliage of South American *Alnus acuminata* is variable, the apices ranging from long-acuminate to very rounded, the bases varying from rounded to long-cuneate, the general shape varying from narrowly lanceolate to broadly ovate, and the pubescence ranging from nearly absent to quite dense.

Alnus castaneifolia Mirbel is a form with extremely narrow leaves having sharp teeth (Figure 33). I have seen only one specimen (and one photograph of a specimen) of this taxon, both collected by Ruiz in Peru. Although this alder may, in fact, represent another subspecies, it seems more likely that it is only a sporadic or local variant of *A. acuminata* ssp. *acuminata*. Without seeing additional material, however, it is impossible to determine this with certainty, and the form is tentatively included in ssp. *acuminata*.

4b. *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furrow

Alnus acuminata ssp. *arguta* (Schlechtendal) Furrow, *Ann. Mo. Bot. Gard.* **63**: 380. 1977; *Betula arguta* Schlechtendal, *Linnaea* **7**: 139. 1832; *Alnus arguta* (Schlechtendal) Spach, *Ann. Sci. Nat. ser. 2*, **15**: 205. 1841; *Alnus arguta* α *genuina* Regel, *Mem. Soc. Nat. Mosc.* **13**(2): 151. 1861. TYPE: *Schiede 21*, "prope San Miguel del Soldado, Naulingo, Acatlan, et Chiconquiaco" (HAL?, not seen; ISOTYPE or ISOSYNTYPE, MO!). Figure 36.

Alnus rufescens Liebman ex Hemsley, *Biol. Centr. Amer. Bot.* **55**: 165. 1882, in part, *pro syn.*

Alnus jorullensis var. *η acuminata* f. *media* Winkler, *Pflanzenreich* **19**(4.61): 127. 1904, in part.

Alnus pringlei Fernald, *Proc. Amer. Acad.* **43**: 62. 1907. TYPE: *Pringle 10125*, Michoacan, by streams near Uruapan, alt. about 1525 m., 13 November, 1905 (HOLOTYPE, GH!; ISOTYPES, DAO!, FI, MEXU!, MICH!, MSC!, NY!, PH!, UCI, US!).

Alnus arguta var. *cuprea* Bartlett, *Proc. Amer. Acad.* **44**: 610. 1909. TYPE: *Pringle 10251*, "Oaxaca: wet canon near base of the summit ridge of the Sierra de San Felipe above the city of Oaxaca" (LECTOTYPE, GH!; ISOLECTOTYPES, DAO!, ENCB!, FI, MICH!, MSC!, UCI, US!).¹

Alnus arguta var. *subsericea* Bartlett, *Proc. Amer. Acad.* **44**: 610. 1909. TYPE: *Pringle 10252*, "Oaxaca: wet canon near the base of the summit ridge of the Sierra de San Felipe, above the city of Oaxaca" (HOLOTYPE, GH!; ISOTYPES, DAO!, ENCB!, FI, MICH!, MSC!, UCI, US!).²

Alnus ovalifolia Bartlett, *Proc. Amer. Acad.* **44**: 611. 1909. TYPE: *Smith 2199*, Guatemala, San Lucas, Dept. Zacatepequez, alt. 5500 ft. (HOLOTYPE, GH!; ISOTYPE, US!).

¹Bartlett does not indicate a type specimen. Of the material cited, *Pringle 10251* best fits the description of the variety and was apparently its primary basis. This collection is therefore chosen as the lectotype.

²Although a type is not designated, this is the only specimen cited in connection with the description of the variety. A paragraph later Bartlett refers *Ghiesbreght 160* from Chiapas to this taxon, but it is clear from the context that he regards *Pringle 10252* as the type.

Alnus ferruginea var. *a. typica* Callier, Mitt. Deutsch. Dendr. Ges. **27**: 161. 1918, in part.

Alnus guatemalensis Gandoger, Bull. Soc. Bot. Fr. **66**: 289. 1919. TYPE: *Von Türrckheim*, "Guatemala, ad Alta Verapaz."³

Narrow-crowned trees up to 30 m in height; trunks usually several, erect, up to 1 m in diameter; young stems dull to moderately lustrous, sometimes slightly to heavily glaucous, the internodes glabrous to moderately villous, the glands small to medium in size and brownish to dark brown. Lenticels of twigs 0.3–1.5 mm long, 0.2–1 mm wide, whitish or yellowish, inconspicuous to moderately prominent. Buds ellipsoid to obovoid, acuminate, acute, or slightly rounded at the apex, moderately to heavily resin-coated; stalk 2–7 mm long, glabrous to moderately villous; scales glabrous to sparsely pubescent. Leaf apex acuminate, acute, or obtuse (rarely rounded); base acute, cuneate, obtuse, or rounded, sometimes oblique; blade (3.5–) 5.5–15 (–16) cm long, 3–8.5 (–11) cm wide; margin slightly to moderately revolute; major teeth 8–14 (–20) mm apart, slightly uneven; secondary teeth (2–) 4–8 (–10) per cm, (0.1–) 0.3–1.5 mm deep, slightly uneven; abaxial surface and veinlets glabrous to moderately villous or (rarely) tomentose. Lateral veins (7–) 10–15 (–18), (3–) 5–8 (–12) mm apart at mid-leaf, straight to slightly ascending. Cross-veins between lateral veins well developed. Petioles (5–) 11–23 (–35) mm long, (0.8–) 1–2 (–2.5) mm in diameter, glabrous to sparsely pubescent. Stipules 4–8 mm long, 1–1.5 mm wide, sparsely pubescent to velutinous. Pistillate inflorescences at anthesis 3–8 mm long, 1.5–3 mm in diameter, on peduncles (1–) 2–5 (–6) mm long, 1–1.5 (–2) mm in diameter; staminate catkins at anthesis (3–) 5–11 (–15) cm long, 5–10 (–11) mm in diameter, on peduncles 2–10 (–17) mm long, 1–1.8 (–2) mm in diameter. Staminate flowers with 4 perianth parts, these obtuse to rounded at the apex, 1.2–1.9 mm long, 0.6–1.2 mm wide, the margin lined with small to minute glands; stamens appearing equal to or longer than the perianth; filaments 1.1–1.8 mm long; anthers 1.2–2 mm long, 0.9–1.7 mm in diameter, the thecae separate for 35–55% of their

³Gandoger provides no collection number or date for the type collection cited. Von Türrckheim collected at least twice at this locality; I have examined his no. 351, collected there in 1886 (MICH!, US!), and his no. II-1013, collected in 1906 or 1907 (F!, MO!, NY!).



Figure 36. Specimen of *Alnus acuminata* ssp. *arguta* (Schlechtendal) Furlow.
Isotype of *Alnus pringlei* Fernald.

length. Infructescences 11–28 (–45) mm long, 8–12 (–15) mm in diameter, on peduncles 0.2–10 mm long, 1–2 mm in diameter; scales 3–4.5 mm long, 3–4.5 mm wide at the apex, 1–1.7 mm wide at the base. Fruits narrowly wing-margined; body 1.5–3 mm long, 1.5–1.8 mm in diameter; wings 2–2.3 mm long, 0.2–1 mm wide, chartaceous to coriaceous; persistent styles 0.5–0.8 mm long. Figures 14A, 15A, 22A, 35, and 36.

DISTRIBUTION AND HABITAT: Mexico from central Sonora southeast along the Sierra Madre Occidental and the Sierra Madre del Sur to Oaxaca; east and north from Michoacan to southern San Luis Potosi and northern Veracruz, and in central Chiapas; southern Guatemala; central Costa Rica and southwestern Panama. Along streams and adjacent moist slopes at elevations from about 2,000 to 3,200 meters (though sometimes found as low as 1,500 or as high as 3,700 meters). Usually with *Pinus*, *Quercus*, or *Abies*. Figure 37.

COMMON NAMES: Aile, jaul, aliso.

REPRESENTATIVE SPECIMENS: **Costa Rica.** Roads above San Isidro de Coronado, *Allen* 548 (F); Las Nubes, Coronado, *Echeverria* 123 (F, UC); Prov. Cartago, Cordillera de Talamanca, *Lems* 5031 (NY); near Sanatorio de Tierra Blanca, Cartago, slopes of Volcán Irazú, *Rodriguez C.* 145 (MICH, UC); bords des rivières su Copez, *Tonduz* 11680 (MEXU, MICH, NY). **El Salvador.** Northern slopes of Santa Ana Volcano, Dept. of Santa Ana, area known locally as “El Comun”, *Allen & Van Severen* 6880 (F); cloud forest Mountain Cerro Verde, Dept. Santa Ana, *Molina R. & Montalvo* 21520 (NY). **Guatemala.** 5 mi N of San Juan Ixcay on road to Soloma, *Breedlove* 8572 (F); bank of Río Panajuchel near Lake Atitlán, *Hatch & Wilson* 288 (F); Antigua, Dept. Sacatepéquez, *Kellerman* 4966 (US); about 11 mi W of Quezaltenango, *King* 3193 (NY, UC, US); road to Iximche Ruins, Tecpán, Dept. Chimaltenango, *Molina R. et al.* 16127 (F); S. Rafael, *Rittier* 55 (US); Dept. of Huehuetenango, *Skutch* 1110 (F, NY); San Lucas, Dept. Zacatepéquez, *Smith s.n.*, M. Apr., 1800 (US); Dept. Guatemala, slopes of Volcá de Pacaya, between San Francisco Sales and the base of the active cone, *Standley* 80553 (F); Dept. Huehuetenango, Aguacatán road, 10 km E of Huehuetenango, *Standley* 82135 (F); Dept. Huehuetenango, about Leguna de Ocubilá, E of Huehuetenango, *Standley* 82695 (F); Dept. San Marcos, mountains along the road between San Marcos and Serchil, *Standley* 85337 (F); Dept. Quezaltenango, Cerro Quemado, *Standley* 86026 (F); Dept. Quezaltenango, above Los Vahos, Cerro Quemado, *Standley* 86107 (F); Dept. Quezaltenango, Volcán Zunil, *Steyermark* 34605 (F); Dept. El Progreso, between Calera and summit of Volcán Siglo, *Steyermark* 43037 (F, NY); Dept. Alta Verapaz, Cobán, 4200 ft., *von Türckheim* 351 (MICH, US); Dept. Alta Verapaz, Cobán, 1350 m, *von Türckheim* II-1013 (F, MO, NY); pine forest region in Sierra Madre Mountains where Depts. of

Huehuetenango, Totonicapán, and Quezaltenango join, *Williams et al.* 22718 (F). **Panama.** Llano del Volcán, *Allen* 3468 (F, MICH, MO, NY, UC); Volcán de Chiriquí, *Davidson* 997 (F); 8 mi NE of El Volcán, *Tyson & Dwyer* 828 (MO); Finca Lérída to Peña Blanca, *Woodson & Schery* 317 (MO). **Mexico.** CHIAPAS. Along road to Zontehuitz, *Breedlove* 6649 (ENCB, F, MICH); along the road to Chenalho near the school house of Yal Ichin, *Breedlove* 7851 (ENCB, F); along creek near road 1 km N of Aguacatenango, *Breedlove* 7909 (ENCB, MICH); on road from San Cristóbal Las Casas to Tenejapa, *Breedlove* 9063 (F, MICH); 1 mi W of Nabenchauk, *Breedlove* 9522 (MICH); creek bank at NE boundary of Aguacatenango, *Breedlove* 9649 (MEXU, MSC, US); SE city limits of Teotisca, *Breedlove* 11300 (MEXU); near the center of Amatenango, *Breedlove* 12150 (MSC); in the barrio of Tuk, paraje of Matsab, *Breedlove* 12457 (MSC); between Las Casas and Tenejapa, *Carlson* 2412 (MEXU, MICH); on the NW side of Muk'ta vits (Cerro Huitepec), *Laughlin* 1870 (MSC); near Zinacantán Center, *Laughlin* 2347 (MEXU); de S. Cristóbal a Buenavista (Chepetic), *Miranda* 4987 (MEXU); Cerro del Boqueron, *Purpus* 6981 (NY, UC); paraje de Mohosik', *Ton* 1134 (MSC); in the paraje of Yash'anal, *Ton* 2130 (MEXU, NY). CHIHUAHUA. Basigochi, SE of Creel, *Knobloch* 498 (ENCB, MSC, WIS); near Concheño, *LeSueur* 594 (F); 44 mi S of Creel, steep barranca wall, *Straw & Foreman* 1901 (ENCB, MEXU, MICH). DISTRITO FEDERAL. On hwy. 16, 1.9 mi W of San Bartolo, *Denton* 1922 (MSC, WTU); Cañada de Contreras, cerca de 2° dinamo, *Espinosa* 641 (ENCB). DURANGO. North slopes of Cerro Huehueto, S of Huachicheles, about 75 mi W of Cd. Durango, *Maysilles* 7257 (MEXU, MICH); San Ramón, *Palmer* 207 (NY, UC, US). GUANAJUATO. Mountains ESE of San José Iturbide and about 5 mi W of Cerro Zamorano, wooded canyons in oak forests near summits called Mesa del Gato, *McVaugh* 10381 (MEXU, MICH); San Luis de la Paz, *Salazar* 5 (MEXU). GUERRERO. Pilas, Distr. Mina, *Hinton* 10705 (NY, UC); approximately 6 mi W of Mazatlán, *Rowell* 3913 (MICH); 2 km al E de Omiltemi, *Rzedowski* 16044 (ENCB); 5 km al W de Camotla, Mun. de Chichihualco de Leonardo Bravo, *Rzedowski* 16405 (ENCB, MEXU, MSC); 11 km al E del Aserradero Agua Fria, *Rzedowski & McVaugh* 260 (ENCB, MSC). HILDAGO. Alrededores de Zacualtipán, *González Quintero* 318 (ENCB, MEXU, MSC); Santiago Tepepa, Mun. de Acoxochitlan, *González Quintero* 493 (ENCB); Rancho Viejo, Mun. de La Mision, *González Quintero* 1005 (ENCB); 30 km al NE de Jacala, *González Quintero* 1337 (ENCB); Xochicoatlan, Mun. de Molango, *González Quintero* 1560 (ENCB); Santuario, 22 km al NNE de Ixmiquilpan, *González Quintero* 2272 (ENCB); cerca de Chapulhauacan, *Rzedowski* 12265 (ENCB, MSC); Lindavista, sobre el camino a Tenango de Doria, *Vela & Rzedowski* 349 (ENCB). JALISCO. Etat de Jalisco, *Liquet s.n.*, without date (NY); mountain in oak-pine forest, near summit of pass 7-8 road mi NW of Los Volcanes along road between Ayulta and Mascota, *McVaugh* 12208 (MICH, US); about 6-10 mi SW of Talpa de Allende, in the valley of Río Charco Verde and near its headwaters, *McVaugh* 14330 (MICH); 10-12 mi W of Talpa de Allende, in the headwaters of an E branch of Río de Talpa, 3 mi above Los Sauces, *McVaugh* 21440 (MICH); headwaters of Río Mascota, about 20 km, airline, SE of Talpa de Allende, *McVaugh* 21474 (MICH); 16 km S of El Chante (ca. 25 km SE of Autlán), *McVaugh* 23055 (ENCB, MICH); Sierra del Halo, near a lumber road leaving the Colima highway 7 mi SSW of Tecalitlan and extending SE toward San Isidro, *McVaugh & Koelz* 1123 (MICH). MÉXICO. Rancho Tobias near Villa Guerrero, *Alexander & Hernandez X.* 1978 (NY); Rancho Santo Tobias near Villa Guerrero, *Gilly* 104 (MSC); along small stream just N of Amecameca, *Gilly & Dodds I* (MSC, NY);

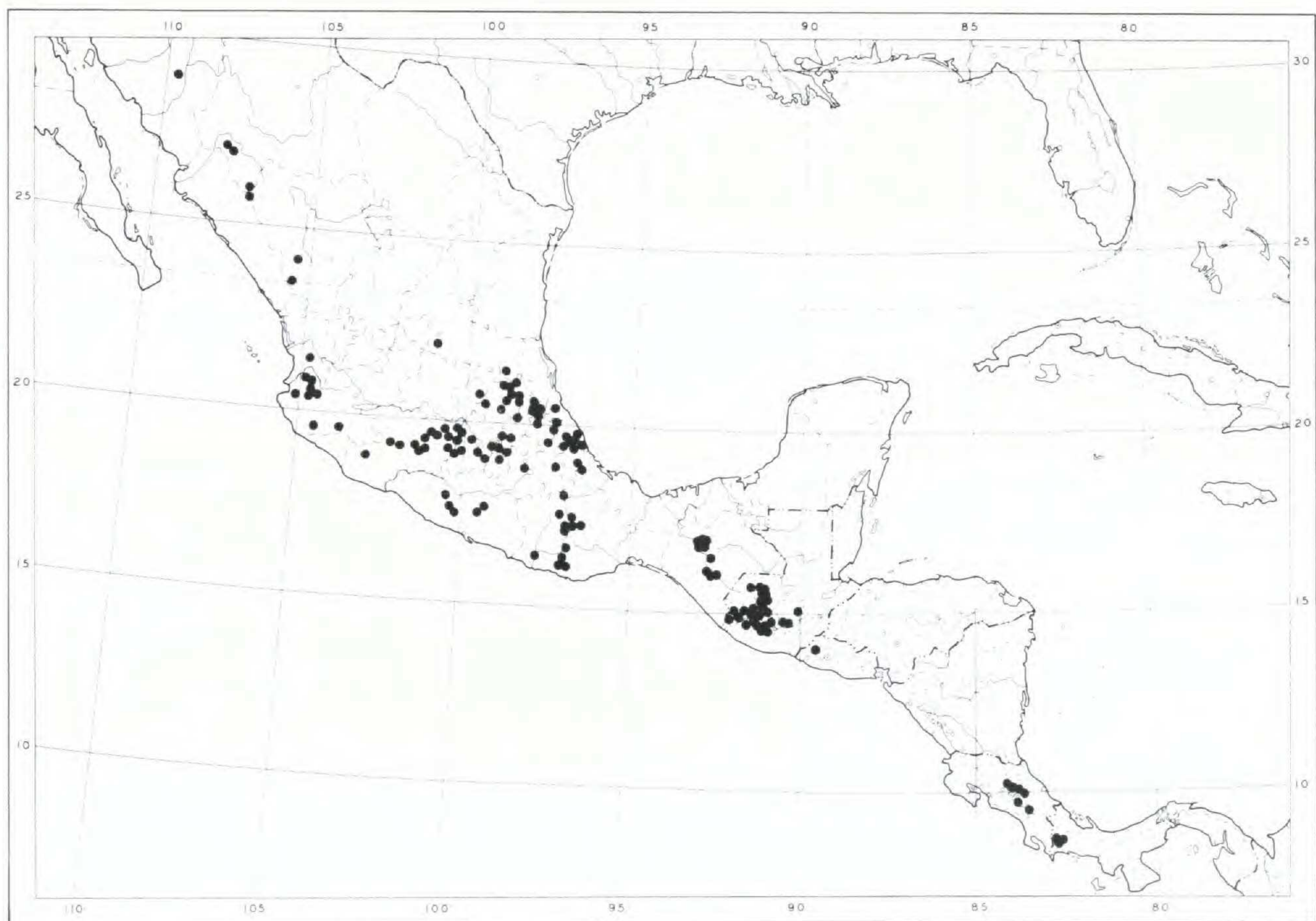


Figure 37. Distribution of *Alnus acuminata* Humboldt, Bonpland, and Kunth ssp. *arguta* (Schlechtendal) Furlow in Mexico and Central America.

Rancho Santo Tobias near the town of Villa Guerrero, *Gilly et al.* 103 (MSC); 5 km SW de Cahuacan, *González Quintero* 870 (ENCB, MSC); La Labor, Distr. of Temascaltepec, *Hinton* 2780 (US); Rincón, Distr. Temascaltepec, *Hinton* 8785 (NY). MICHOACÁN. South of Morelia at km 263, *Barr* 63-586 & *Niles* 313 (UC); 1.5 km S of Opopeo, *Furlow* 337 (MSC); Zitácuaro-Carpinteros, *Hinton* 11875 (DS, NY, UC); west-facing slopes of Cerro de Carboneras above the Río Cupa, *King & Soderstrom* 4893 (MICH, NY, UC); 8-10 mi NW and WNW of Ciudad Hidalgo, along mountains W of Cerro San Andrés and 6-7 mi N of village of San Pedro Aguaro, *McVaugh* 9992 (MEXU, MICH, MO); San José Purua, *Paray* 2203 (ENCB); by streams near Uruapan, 5000 ft, *Pringle* 10125 (DAO, F, MEXU, MICH, MO, MSC, PH, UC, US); 14 km al E de Zitácuaro, sobre la carretera a Toluca, *Rzedowski & de la Sota* 18324 (ENCB, MEXU). MORELOS. Al N de Coajomulco, *Palacios s.n.*, Jan. 9, 1965 (ENCB). NAYARIT. 5 mi N of Compostela, near the bridge over Río Miravalles, *McVaugh & Koelz* 627 (MICH). OAXACA. San Miguel Suchistepec, *Alexander* 596 (MEXU); between Ayulta and Santa Maria, *Camp* 2751 (MICH, NY, UC); Cerro San Felipe, *Conzatti* 2215 (F); Hacienda Guadalupe, *Conzatti e hijos* 4768 (MICH); vicinity of Cerro Zempoaltepetl, *Hallberg* 943 (ENCB, MICH); Cerro de San Felipe, *Mexia* 9121 (F, MO, NY, UC, WTU); by brooks, Sierra de San Felipe, *Pringle* 10251 (DAO, ENCB, MICH, MSC, UC, US, WIS); by brooks, Sierra de San Felipe, *Pringle* 10252 (DAO, ENCB, F, MICH, MSC, UC, US, WIS); Puertecillo de Lanchao, *Rzedowski* 19624 (ENCB, MEXU, MSC). PUEBLA. Huauchinango, *Aguirre & Reko* 150 (NY); entre Teziutlán y Atempan, *Ern* 434 (ENCB); 5 km al SW de Huauchinango, *Espinosa* 601 (ENCB, MEXU); Los Molinos, near Atlixco, *Gilly* 128 (MSC); Teziutlán, *Orcutt s.n.*, Sept. 6, 1910 (F, MO); Sierra de Zacapoaxtla, *Palacios s.n.*, Jan. 19, 1968 (ENCB); El Paraiso, V. Juarez, *Sarukhan et al. s.n.*, Apr. 12, 1962 (MEXU). QUERETARO. 51 mi NE of Zimapan, *Waterfall* 14209 (US). SAN LUIS POTOSÍ. El Guajolote, 10 km al W de Rosa de Castilla, *Rzedowski* 8529 (ENCB). SINALOA. Along the Arroyo El Surutato, 2 mi N of Surutato, Sierra Surutato, *Breedlove* 16484 (MICH); 3 mi N of Los Ornos along road to Ocurahui, *Breedlove & Thorne* 18415 (MICH). SONORA. Horconcos, Río Huachinera, *White* 2965 (ARIZ, MEXU, MICH). VERACRUZ. Orizaba Mexique, *Bilimek* 404 (NY); 32 km SW of the city of Orizaba, *Furlow* 341 (MSC); San Miguel del Soldado E de Jalapa, *Gomez-Pompa* 1472 (MEXU); orillas del Río Jamapa, cerca de Ixhualtlan del Cafe, *Lot* 882 (GH, MEXU); Acatlan, *Rosas R.* 600 (GH); Malpais, entre la Joya, Ver. y Rancho Dos Hermanos, Ver., *Vela Galves* 108 (ENCB); Champilico, *Ventura A.* 58 (ENCB, MSC); La Florida, Mun. de Atzalan, *Ventura A.* 243 (ENCB, MSC); valley NW of La Perla (vicinity of Orizaba), *Weaver et al.* 1700 (MICH).

Several variants of *Alnus acuminata* ssp. *arguta* have been treated as separate species or varieties of *Alnus arguta*. One such taxon is *Alnus pringlei* Fernald, which differs from ssp. *arguta* mainly in that the petioles and veins of the leaves are more densely pubescent. *Alnus arguta* var. *subsericea* Bartlett, *A. arguta* var. *cuprea* Bartlett, and *A. ovalifolia* Bartlett, similarly, represent minor variations in leaf shape and indumentum characters. Throughout the range of this subspecies, infructescences vary considerably, both in length and diameter. The leaves are almost always ovate, though they

sometimes become elliptic or (infrequently) even obovate, and the apices range from acuminate to rounded. Pubescence on the abaxial leaf surface varies from absent to very dense. Leaf surface glands may appear either large and densely-arranged or smaller and sparser. The glands are never entirely absent, however, contrary to the statements of Fernald (1904b), Standley (1920), and Standley and Steyermark (1952).

Alnus acuminata ssp. *arguta* is most easily distinguished from ssp. *acuminata* by its coarser more deeply toothed leaves. The leaves of ssp. *acuminata* are often toothless or nearly so, while this is only infrequently the case in ssp. *arguta*. The foliage of ssp. *acuminata* is also somewhat broader and more elliptical than that of ssp. *arguta*.

This subspecies occurs throughout much of the mountainous parts of Mexico and northern Central America. Small disjunct populations are also found in Costa Rica and Panama (Furlow, 1977), and specimens from these areas are to a certain degree distinct from those of both Mexico and South America. Sometimes the leaves approach *Alnus jorullensis* in shape and indumentum, though they retain the overall aspect of *A. acuminata*. It is difficult to place these populations in a particular subspecies. However, numerical analysis (unpublished, to be presented in a later paper) indicates that they possess somewhat stronger affinities with ssp. *arguta* than with ssp. *acuminata*. They are thus treated here as belonging to ssp. *arguta*.

Alnus acuminata ssp. *arguta* is usually found growing along mountain streams or on moist slopes in pine-oak forests at relatively high elevations in Mexico and northern Central America. Toward the south of its range it shows a preference for moderate moisture conditions, being largely absent on the Pacific Slope, where rainfall is more abundant (Standley & Steyermark, 1952).

4c. *Alnus acuminata* ssp. *glabrata* (Fernald) Furlow

Alnus acuminata ssp. *glabrata* (Fernald) Furlow, Ann. Mo. Bot. Gard. **63**: 381. 1977; *Alnus glabrata* Fernald, Proc. Amer. Acad. **40**: 26. 1904. TYPE: *A. Dugès* s.n., April, 1882, "Monte San Nicolas, Guanajuato" (Lectotype of Standley, (GH!), 1920). Figure 38.

Alnus jorullensis var. *η acuminata* f. *media* Winkler, Pflanzenreich **19**(4.61): 127. 1904, in part.

Alnus glabrata var. *durangensis* Bartlett, Proc. Amer. Acad. **44**: 611. 1909. TYPE: Palmer 965, in the vicinity of the City of Durango, State of Durango, April to November 1896 (HOLOTYPE, GH!; ISOTYPES, FI, NY!, UC!, US!).

Narrow-crowned trees up to 30 m in height; young stems dull to slightly lustrous, not glaucous to moderately glaucous; internodes glabrous, moderately glandular; lenticels 0.3–1 mm long, 0.2–0.7 mm wide, whitish or yellowish, moderately prominent; leaf scars 1–1.5 mm high, 1.5–2.5 mm wide. Buds ovoid to ellipsoid, slightly rounded to rounded at the apex, moderately to heavily resin-coated; stalk 2–6 mm long, 1–2 mm in diameter, glabrous, densely glandular; body 5–9 mm long, 3–4 mm in diameter. Leaves narrowly ovate to lanceolate (or rarely elliptic), the apex long-acuminate (or sometimes acute), the base acute to obtuse or rounded; blade (3–) 6–13 (–15) cm long, (2–) 3–6.5 (–8) cm wide, medium to dark green above, light to medium green (or brown) below, chartaceous; margin flat, unthickened, usually sharply double-serrate; major teeth 8–16 (–18) mm apart at mid-leaf, 2–5 mm deep, regular, usually more or less acuminate; adaxial surface glabrous; abaxial surface and veinlets glabrous (rarely very sparsely pubescent), moderately to densely glandular; major veins and vein axils near the base glabrous to sparsely pubescent; pubescence, when present, whitish to pale yellowish. Lateral veins 8–13, 4–8 (–11) mm apart at mid-leaf, straight or slightly ascending; cross veins between lateral veins poorly developed. Petioles (8–) 12–21 (–27) mm long, 0.8–1.5 mm in diameter, glabrous. Stipules 7–9 mm long, 1–2 mm wide, green to light brown, sparsely to moderately pubescent, the hairs yellowish, moderately glandular, the glands yellowish. Pistillate inflorescences at anthesis 4–6 mm long, 2–3 mm in diameter, on peduncles 1–4 mm long, 1–1.7 mm in diameter; staminate catkins at anthesis 6.5–9.5 cm long, 6–8 mm in diameter, on peduncles 2–14 mm long, 1–2 mm in diameter. Staminate flowers with 4 perianth parts, these elliptic to obovate, the apex obtuse to rounded, 1.5–2.1 mm long, 0.8–1.1 mm wide, the margin lined with minute to small glands; stamens usually appearing equal to or longer than the perianth, the filaments 1–1.7 mm long, the anthers 1.6–1.8 mm long and 1.5–1.8 mm in diameter, the thecae separate for 35–45% of their length. Infructescences (10–) 15–25 (–30) mm long, 6–12 (–15) mm in diameter, on peduncles 0.2–3 mm long, 1.2–1.8 mm in diameter; scales 4.5–5 mm long, 3.7–5 mm wide at the apex, 1.2–1.5 mm wide at the base, the apex moderately thickened, the terminal lobe-tip acute to rounded, often somewhat extended. Fruits narrowly wing-margined; body 2.2–4 mm long, 1.2–2 mm in diameter; wings 2.5–3 mm long, 0.3–0.8 mm wide, firm to coriaceous; persistent styles 0.6–1 mm long. Figures 15B, 16C, 38, and 39.



Figure 38. Lectotype of *Alnus glabrata* Fernald (= *Alnus acuminata* ssp. *glabrata* (Fernald) Furlow).

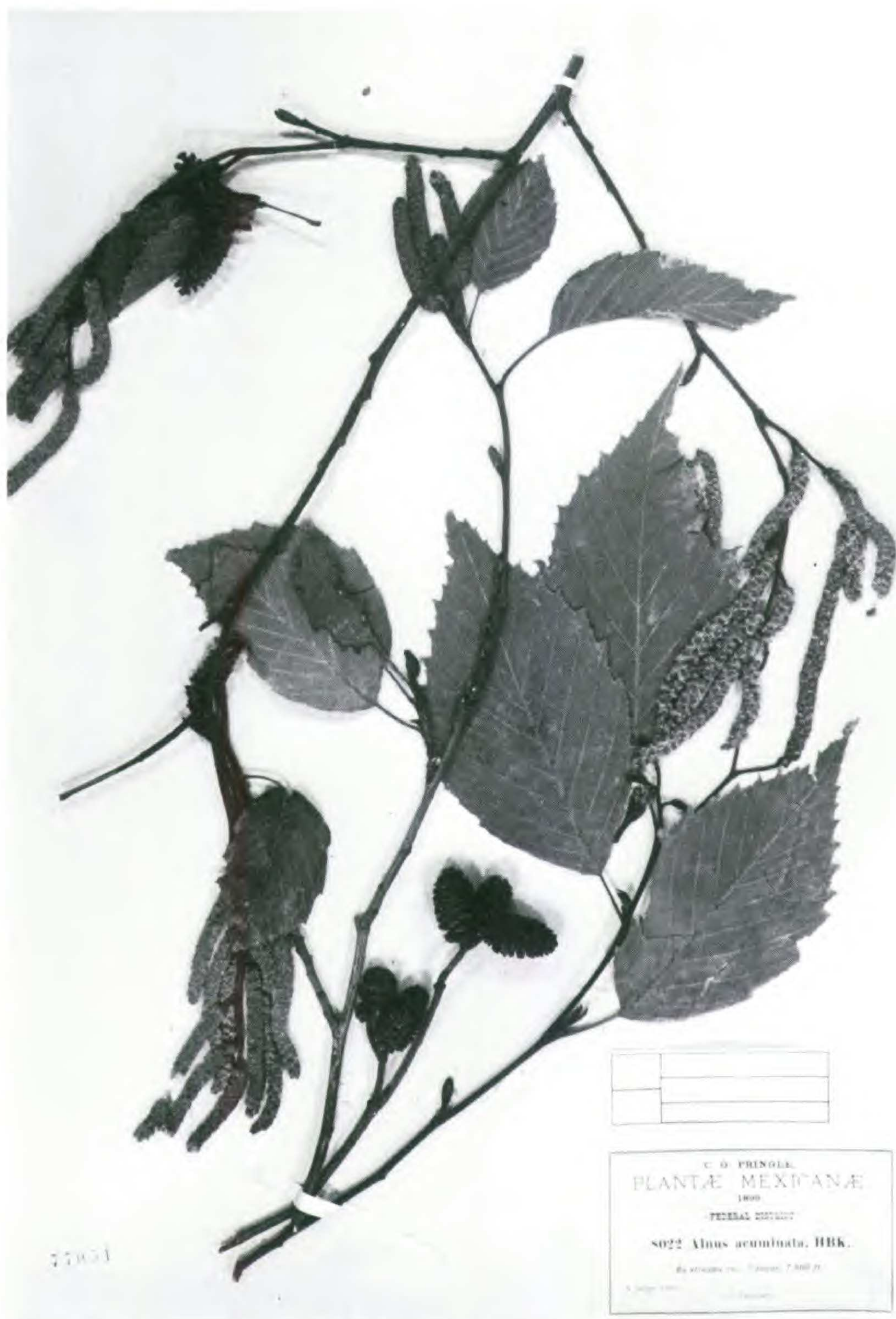


Figure 39. Representative specimen of *Alnus acuminata* ssp. *glabrata* (Fernald) Furlow.

DISTRIBUTION AND HABITAT: Central Durango southeast to Guanajuato, México, Tlaxcala, and north-central Oaxaca. Usually found along streams and on moist slopes, often with *Pinus* and *Quercus*, at elevations from 1,500 to 2,500 (or rarely to 3,000) meters. Figure 40.

COMMON NAMES: Aile, aliso.

REPRESENTATIVE SPECIMENS: **Mexico.** DISTRITO FEDERAL. By streams, Valley of Mexico, *Pringle* 4361 (F, MO, MSC, NY, UC); by streams near Tizapán, 7500 ft, *Pringle* 8022 (F, MEXU, MO, MSC, NY, UC); San Angel, *Torres* 354 (MEXU). DURANGO. At the city of Durango and vicinity, *Palmer* 965 (F, NY, UC, US). GUANAJUATO. Monte de San Nicolas, *Dugés s.n.* in 1882 (GH); 14.5 mi from Guanajuato on the road to Dolores Hidalgo, *Johnston* 2641 (MEXU, MICH, MSC); ca 15 mi from Guanajuato on road to Dolores Hidalgo, *Solbrig & Ornduff* 4509 (UC). GUERRERO. Petlascala, *Mexia* 8979 (F, MO, NY, UC). HIDALGO. Barrancas W of El Salto Station, Distr. Tula de Allende, *Moore* 1457 (MEXU, MICH, UC); Tula, *Rose* 8330 (NY). MÉXICO. Atlacomulco, *Detling* 8920 (ENCB); just N of Amecameca, *Gilly & Dodds* 2 (MSC, NY); Parque Nacional "Los Remedios", *Rzedowski* 19301 (ENCB, MSC); 2 km al SE de San Pablo Ixayoc, *Rzedowski* 24161 (ENCB, MSC). OAXACA. 5 km adelante de Tlaxiaca, *Pennington & Sarukhan K.* 9216 (NY); Rancho del Cura cerca de Concepción, Buenavista, Distr. de Coixlahuaca, *Rzedowski* 25713 (ENCB); 1 km al E de Ihuitlan Plumas, *Rzedowski* 26680 (ENCB, MSC). PUEBLA. Vicinity of Puebla, *Arsene* 135 (US); alrededores de Atzala, *Ern* 328 (ENCB); Los Molinos near Atlixco, *Sharp* 45406 (MEXU). TLAXCALA. Rancho Nuevo, Tlaxco, *Aguilar* 8-A-42 (ENCB); 4 km al W de Apizaco, *Ruiz Bedolla s.n.*, July 9, 1967 (ENCB); orillas del Río Zahuapan, cerca de Tlaxcala, *Weber* 169 (ENCB).

In describing *Alnus glabrata*, Fernald (1904b) did not designate one of his cited specimens as the type. In 1920, Standley, in *Trees and Shrubs of Mexico*, listed the type of this species as from "Monte San Nicolas, Guanajuato," thus establishing one of Fernald's elements (*A. Dugés s.n.*, April, 1882) as the lectotype. This specimen is the first listed by Fernald in the protologue, and its selection by Standley may represent an arbitrary choice of the first listed element, as explicitly prohibited in the Rules of Nomenclature (Stafleu *et al.*, 1972). Without stronger evidence of this, however, the specimen of Dugés should be allowed to stand as the lectotype.

This subspecies occurs at generally lower elevations than ssp. *arguta*, but the habitats of the two overlap altitudinally, and they are sometimes found growing in close proximity. It may eventually prove to be only a minor variant of ssp. *arguta*, but from the material seen, it appears distinct enough to be given subspecific

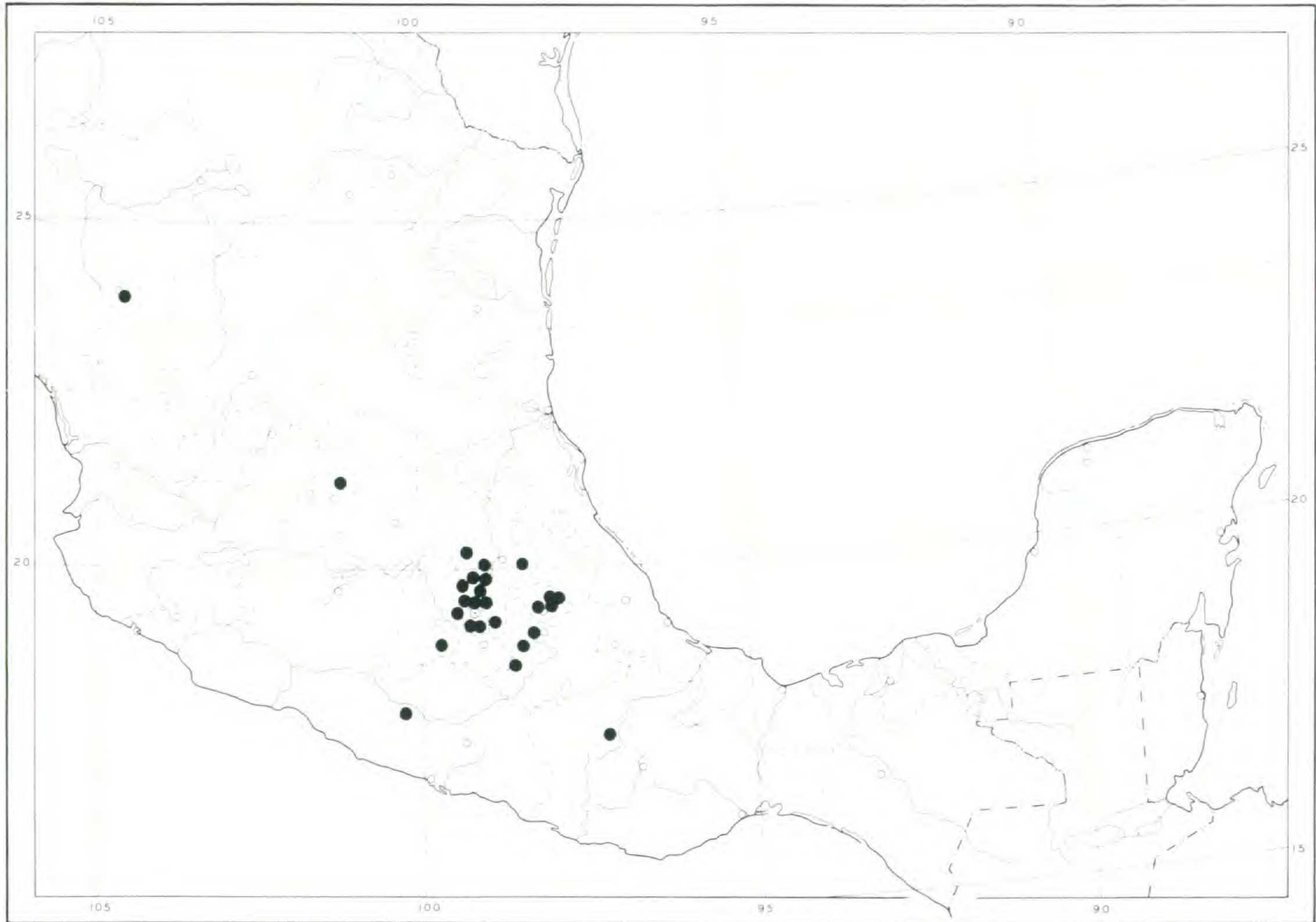


Figure 40. Distribution of *Alnus acuminata* ssp. *glabrata* (Fernald) Furlow.

status. The most useful distinguishing characters are the completely (or nearly) glabrous lower leaf surface and the lanceolate or narrowly ovate, acuminate, sharp-toothed leaf form.

There is abundant evidence of natural hybridization between spp. *glabrata* and *arguta* throughout the range, as shown by numerous specimens having intermediate leaf shapes and indumentum. Where such putative hybridization occurs, it is often difficult to determine these taxa. In the specimens cited here, such intermediates have been assigned to one variety or to the other, depending on their closest affinity. They have not been taken into consideration in constructing the key.

To be concluded in Vol. 81, No. 825 (April, 1978)